REPRODUCTIVE BIOLOGY OF LONGFIN DACE (*AGOSIA CHRYSOGASTER*) IN A SONORAN DESERT STREAM, ARIZONA

by

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ABSTRACT

The longfin dace, Agosia chrysogaster Girard, is the most abundant native minnow of low elevation (< 1,500 m) streams in Arizona, parts of southwestern New Mexico, and northern Mexico. Reproductive life history of longfin dace was examined over a 12-month period (1977-78) in Aravaipa Creek, Graham and Pinal counties, Arizona. Adult males and females are sexually dimorphic, clearly distinguishable by differences in size of fins. Gravid females and tuberculate males persisted throughout the year and spawned in shallow saucer-shaped depressions in sand-bottomed backwaters and runs. Although individual spawning activity was asynchronous, populations reached peak spawning condition at least twice within the year. Peak reproductive activity was during increased discharge in spring and late summer. Fecundity was primarily a function of size. Ovary weight was highly correlated with fecundity and was the most reliable indicator of total mature ova produced.

ACKNOWLEDGEMENTS

Completion of this research project was made possible through the efforts of several individuals to whom I wish to express my sincere appreciation. In particular, I wish to acknowledge W. L. Minckley, my committee chairman, for guidance and assistance I received throughout all phases of my graduate program. He and other members of my committee, John N. Rinne and David I. Rasmussen, provided helpful suggestions and thoughtful criticisms in critical review of this manuscript. David T. Shaffer and Brian A. Millsap deserve special thanks for their advice and assistance regarding computer analysis. Permits for collection of fishes were granted by Arizona Game and Fish Department, and access and other assistance were provided by Defenders of Wildlife (George Whittell Wildlife Preserve) and U. S. Bureau of Land Management (Aravaipa Canyon Primitive Area).

Finally, I wish to thank my wife and best friend, Lauren, for her constructive criticism, field and technical assistance, and the unwaivering support and encouragement she offered during the course of this study.

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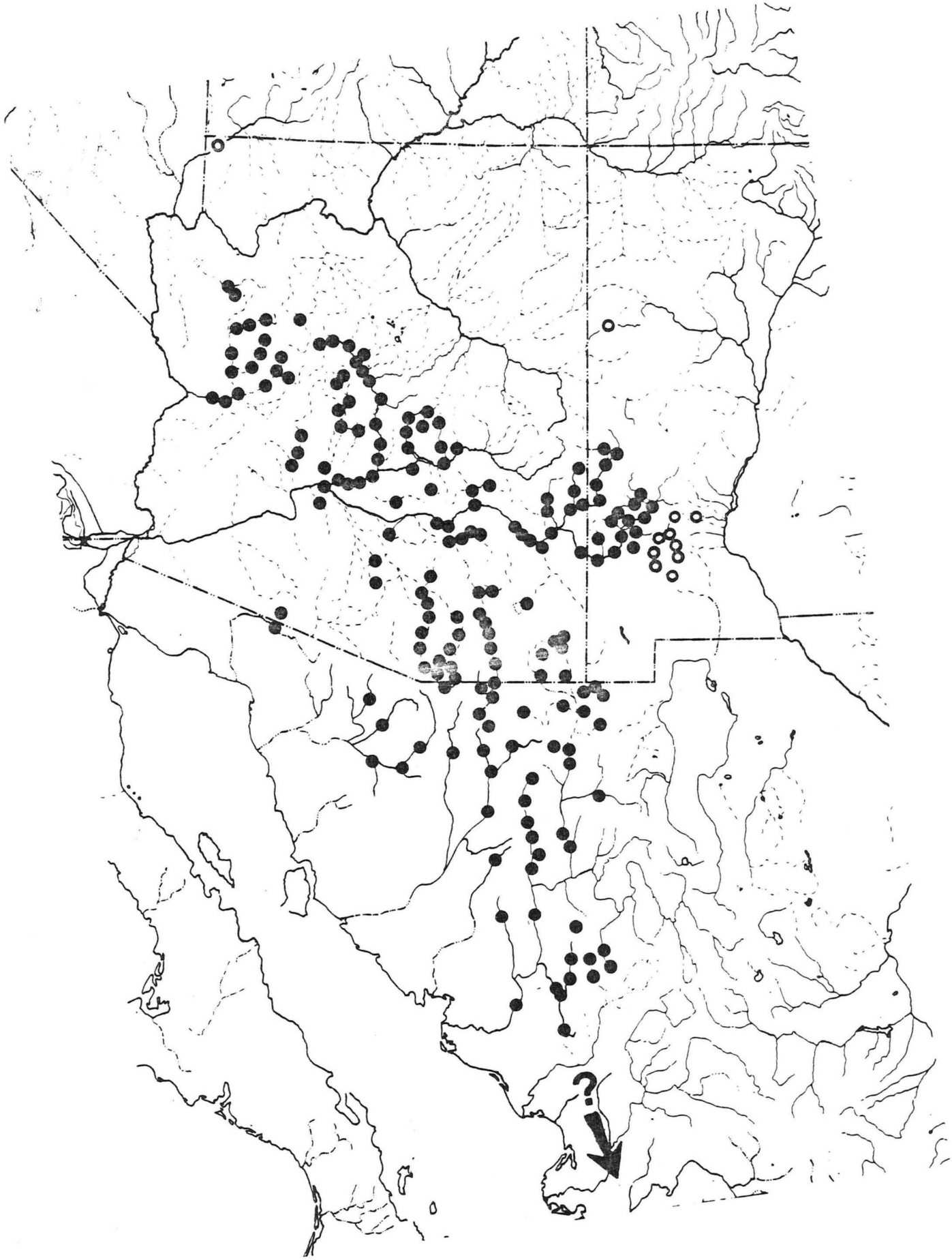
INTRODUCTION

The longfin dace, Agosia chrysogaster Girard, is the most common native cyprinid of low elevation desert streams in the arid American Southwest (Koster, 1957, Branson et al. 1960, Minckley and Barber 1971, LaBounty and Minckley 1972). A. chrysogaster was originally described from the Gila River drainage, and is monotypic. However, recent authors recognize at least one other distinct form in northwestern Mexico (Miller 1958, Miller and Lowe 1964, McNatt 1974, Minckley 1980, Hendrickson et al. 1981). Longfin dace naturally range from the Hualapai (Red) Lake drainage, northwest Arizona (original data), southward at least to the Rio Sinaloa basin, Sinaloa, Mexico (Minckley 1980; Fig. 1). They have been introduced, with limited success, into other systems, i.e. Zuni and Mimbres rivers, New Mexico (Koster 1957), Virgin River, Arizona (Minckley 1973), and the Rio Grande basin, New Mexico (Huntington and Roberts 1959, Minckley 1973).

Longfin dace typically inhabit shallow, sand-bottomed runs with laminar flow. They often frequent cover provided by overhanging vegetation, algal mats, or undercut banks. A. chrysogaster ranges in altitude from near sea level in coastal streams of Mexico (Hendrickson et al. 1981) to almost 2,300 meters (m) in the Gila River headwaters, New Mexico (Minckley 1981); they are rarely abundant above 1,500 m (Minckley 1973). They are diurnal feeders and opportunistic omnivores (Fisher et al. 1981). Major food items in addition to algae and detritus include aquatic insects, primarily baetid mayfly nymphs and

Figure 1. Distribution of Agosia chrysogaster (open circles represent transplanted populations). Modified from Lee et al. (1980) with permission.



chironomid dipteran larvae associated with drift (Schreiber 1978, Schreiber and Minckley 1982).

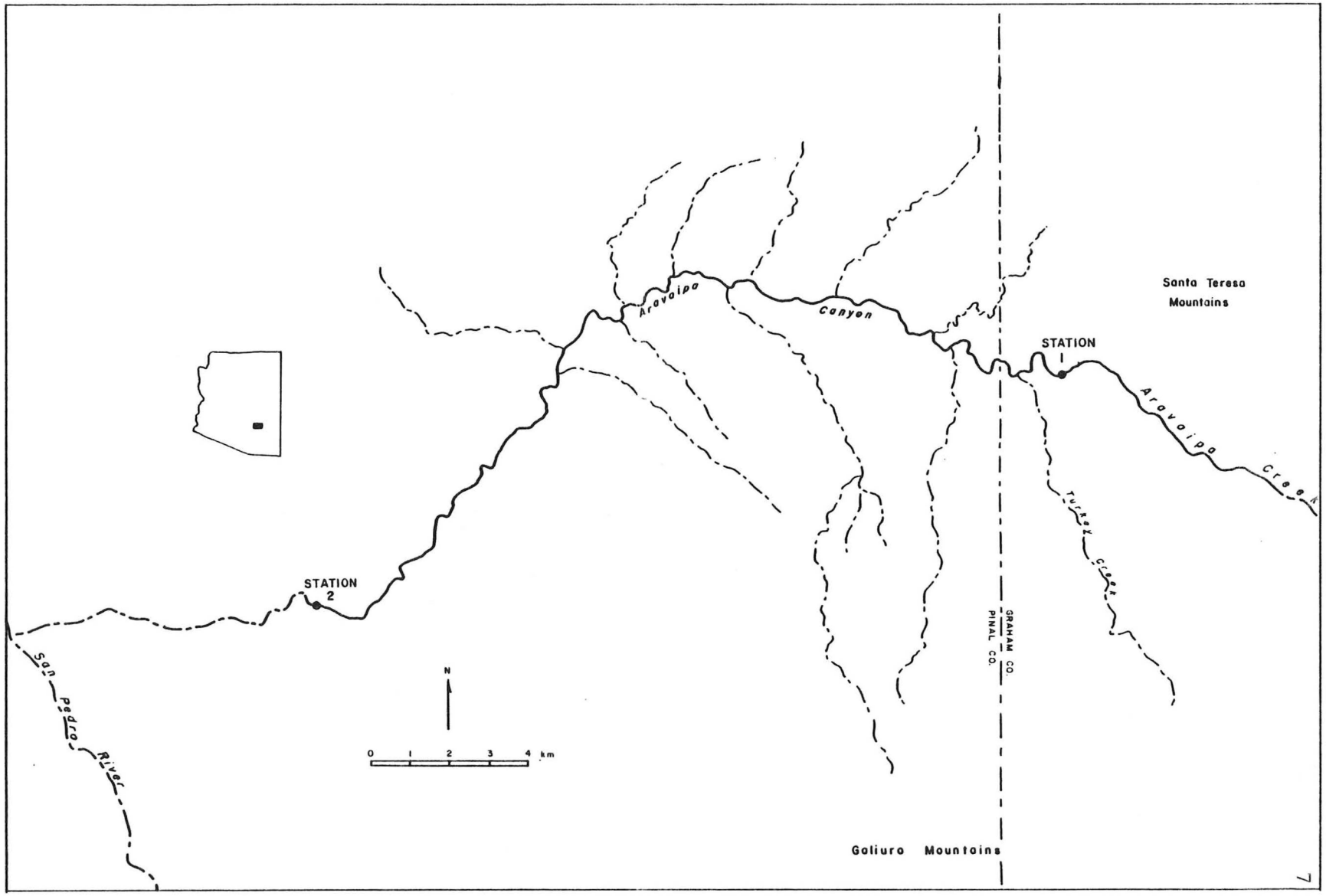
Despite its early discovery (Girard 1856), widespread distribution (Minckley 1980), and historical and current abundance (Miller 1961, Minckley and Barber 1971), surprisingly little has been published on the biology of this fish (Lowe et al. 1967, Minckley 1969, 1973, 1980, Stout et al. 1970, Minckley and Barber 1971, Rinne 1975, Lewis 1978a, 1978b, Schreiber 1978, Constantz 1981, Fisher et al. 1981, Schreiber and Minckley 1982). Most publications have dealt with general ecology, and have lacked detailed information on spawning periodicity and fecundity. The present study was initiated to ascertain that information and thus contribute to specific life history data for A. chrysogaster.

DESCRIPTION OF THE STUDY AREA

Aravaipa Canyon, Graham and Pinal counties, Arizona, is collectively managed by the U.S. Bureau of Land Management (USBLM) as a Primitive Area and by the Defenders of Wildlife as the George Whittell Wildlife Preserve. Stream reaches above and below the canyon are in private holdings. The watershed has been studied by a number of investigators, particularly for its ichthyofauna. References for general and specific descriptions of the drainage include Barber and Minckley (1966, 1982), Barber et al. (1970), USBLM (1970, 1979), Minckley and Barber (1971), Deacon and Minckley (1974), Smith (1974), Bruns (1977), Schreiber (1978), Bruns and Minckley (1979), Siebert (1980), Minckley (1981) and Schreiber and Minckley (1982).

Aravaipa Creek drains 1,401 square kilometers (km^2) before entering the San Pedro River (Gila River basin) at an elevation of 658 m (Fig. 2). Origin of surface flow is 6.5 km northwest of Klondyke at 1,010 m. Surface flow during periods of modal discharge is maintained for 40 stream-km before receding into alluvium 7.6 km from the San Pedro River (elevation 701 m). Aravaipa Creek is characterized by riffle, pool, and run habitat types, with runs most representative. Channel widths vary from 5 to 100 m and are narrowest within Aravaipa Canyon. Stream width and gradient average 10 m and 8.3 m/km, respectively (Minckley 1981). Steepest gradients are within Aravaipa Canyon as are maximum depths of ca. 1 m. Beyond the Canyon, stream depth averages less than 10 centimeters (cm). Aravaipa Creek typically flows over fine (sand/gravel) alluvial sediments and meanders as a single or braided channel.

Figure 2. Sketch map of Aravaipa Creek, Graham and Pinal counties, Arizona, with location of sampling stations.


Aravaipa Canyon
STATION 1
STATION 2
Aravaipa Creek
Turkey Creek
Santa Teresa Mountains
GRAHAM CO.
PINAL CO.
San Pedro River
Galiuro Mountains
N
0 1 2 3 4 km

Mean discharge at a gaging station 10 km upstream from the San Pedro River, is 0.72 cubic meters/second (m^3/s), but varies from a low of 0.008 m^3/s (30 August 1940), to a maximum of 566 m^3/s (2 August 1919) (n = 24 years; USGS 1979b). Average discharge during the current study was 1.13 $\pm$ 3.84 m^3/s (n = 365 days)[1/]. Flash flooding is normally associated with a bimodal pattern of winter and summer precipitation peaks typical of the Sonoran Desert.

Water quality in Aravaipa Creek is within levels outlined in federal and state surface water standards (Sommerfeld 1981). Disturbance within the USBLM Primitive Area is minimal and impacts of livestock grazing, temporary impoundments, and irrigation diversions on private lands only locally influence the stream. Water temperatures range between 4.2° C in January to 33.5° C in August. Maximum daily variations are only slightly greater in summer (12.5° C) than winter (11.5° C) (Minckley 1981). Water temperature variations in Araviapa Creek are influenced by a number of factors including discharge volume, relative humidity, angle of incident radiation, daylength, meteorological conditions, subterranean inflow from the aquifer, and particularly canyon and riparian shading.

Riparian vegetation in the upper reaches of Aravaipa Creek includes mixed broadleaf species such as cottonwood (Populus

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[1/]Mean followed by $\pm$ one standard deviation, as used throughout text and tables.

fremontii), willow (Salix gooddingii, S. bonplandiana), sycamore (Plantanus wrightii), velvet ash (Fraxinus pennsylvanica), walnut (Juglans major), box elder (Acer negundo), and Arizona alder (Alnus oblongifolia) (Kepner 1981). Middle reaches are dominated by cottonwood/willow communities, and downstream reaches are vegetated by winter-deciduous microphylls, mostly bosque-type species such as mesquite (Prosopis velutina) and catclaw (Acacia greggii). The streamside understory in all communities is dominated by seep willow (Baccharis salicifolia). Watercress (Rorippa nasturtium-aquaticum) and monkey flower (Mimulus dentilobus) are the two major aquatic vascular plants associated throughout the creek.

Aravaipa Creek maintains a predominately native ichthyofauna including five cyprinids: longfin dace, speckled dace (Rhinichthys osculus), spikedace (Meda fulgida), loach minnow (Tiaroga cobitis), and roundtail chub (Gila robusta); and two catostomids: Sonora sucker (Catostomus insignis) and desert sucker (Pantosteus clarki). Green sunfish (Chaenobryttus cyanellus) is the only non-native form that has persisted since its introduction. Longfin dace historically have been the most numerically abundant species in Aravaipa Creek (Minckley 1981).

METHODS AND MATERIALS

Two sampling stations were established on Aravaipa Creek (Fig. 2), one above the Canyon (Station 1: T6S, R19E, NW1/4 SW1/4 Sec. 20; elevation 946 m) and one below (Station 2: T7S, R17E, NE1/4 NW1/4 Sec. 8; elevation 704 m). Station 1 was a shallow sand/gravel run shaded by riparian vegetation (mostly Goodding and seep willow). Station 2 was a sand-bottomed run with little or no shading. Riparian vegetation consisted of mesquite and seep willow at the lower station.

Monthly fish collections at both stations were made from September 1977 through August 1978 by 115 volt, A.C., backpack electrofishing equipment and 3.2 mm-mesh nylon seines. All specimens were preserved in 10% formalin and transferred to 50% isopropanol. A total of 1,491 Agosia chrysogaster was collected. With the exceptions of certain morphometric features and patterns of tuberculation related to determination of sexual dimorphism, males are not further considered in the present report.

Females comprised slightly more than half of the total collection ($n = 780$, 64 ± 20 per month). All were measured to the nearest 0.01 millimeter (mm) for total length (TL) and wet-weighed to the nearest 0.01 gram (g) on a Mettler analytical balance. An equation to predict standard length (SL) from TL ($SL = -3.037 + 0.863\ TL$) was developed by regression analysis ($r = 0.998$, $p < 0.001$) based on paired measurements of 165 specimens. Ovaries were excised, retained in 4% formalin (Scott 1962), and wet-weighed to the nearest 0.1 milligram (mg). Lengths and weights were not corrected for possible changes due

to preservation. Three-hundred-seventy-two females were dissected from Station 1 and 400 from Station 2.

Spawning periodicity was determined from gonadosomatic or maturity indices (MIs) (Vladykov 1956, Williams 1959), where the ratio of ovary weight to body weight (including ovaries) is expressed as a percentage. Fecundity was determined by enumerating ova and measuring ovum diameters. Ova were divided into three distinct classes: Class III, immature ova; Class II, maturing ova; and Class I, ripe ova. Class III ova were approximately 0.2 to 0.8 mm diameter, yolkless, white, and opaque; Class II ova were yolked, opaque, and approximately 0.8 to 1.2 mm; and Class I ova were greater than 1.2 mm, yellow, with a transparent perivitelline space. Class III ova outnumbered both Classes I and II combined. All ova greater than 0.19 mm in diameter were counted and measured in 41 specimens.

Ovaries were teased apart in Petri dishes under a dissecting scope and ovum diameters measured using a 0.2-mm gridded matrix on an Eberbach scale projector. Measurements were recorded on cassette tapes and later tabulated. A total of 64,984 ova was counted and measured.

In addition to spawning periodicity and fecundity, various physical and biological information was gathered on spawning behavior of A. chrysogaster. Data were obtained for nest size and location, size at hatching, nuptial tuberculation, sexual dimorphism, and sex ratios.

Compilation and analysis was performed either on a Honeywell 6680 computing system at the USBLM Denver Service Center or a T1-51-II

handheld calculator. All specimens not sacrificed for dissection were deposited in the Collection of Fishes, Arizona State University, Tempe (ASU 8568-8575 and 8592-8607).

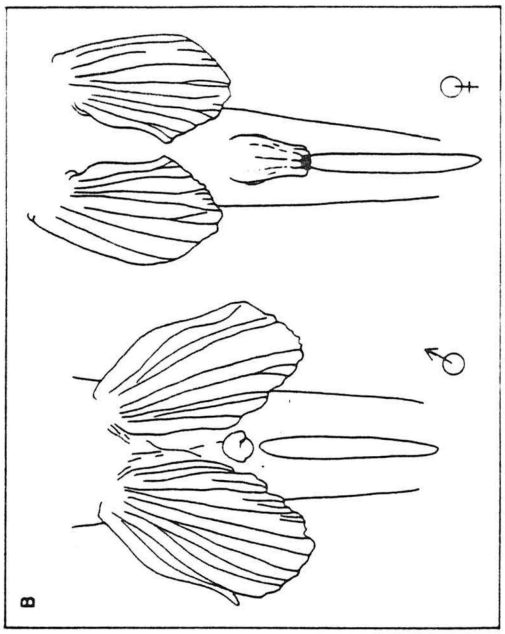
RESULTS

Sexual Dimorphism

Meristic characters in Agosia chrysogaster are similar between sexes. However, males could readily be separated from females on the basis of morphological differences and intensity of tuberculation. Males have markedly contrasting blacks and whites (or silvery) on the body, as opposed to a generally drab coloration of females. Their fins, in addition to becoming longer as demonstrated by measurements (see below) are far more expansive and distally rounded than those of females. The anal fin of the female is an exception, being longer and more accuminate than that of the male (Fig. 3A). A further difference is in appearance of the urogenital papillae (Fig. 3B). The urogenital papilla in females is an enlarged, fleshy, protuberant structure that extends well away from the body. In males the structure is less developed, rarely extending beyond the body contour.

Selected, sexually mature males and females were measured for 13 morphometric characters (Table 1). Data were analyzed using one-way analysis of variance (ANOVA) techniques to determine significant ($p < 0.01$) dimorphic characters. Only 7 of 13 characters were significantly different at the 0.01 level (Table 2). The highest significant F-scores ($F > 14.0$, $p < 0.001$) were for lengths of depressed dorsal fin ($F = 129.49$) and pelvic fin ($F = 88.82$). Lowest were for body weight ($F = 11.04$) and body depth ($F = 9.65$). In almost all cases, excepting body weight, body depth, and anal fin length, features of males were larger than females. Body weight and depth obviously were greater in females due to presence of mature ova.

Figure 3. Sexual dimorphism in Agosia chrysogaster: A) male 66.5 mm TL above, female 75 mm TL below (scalation and nuptial tubercles omitted); B) urogenital papillae.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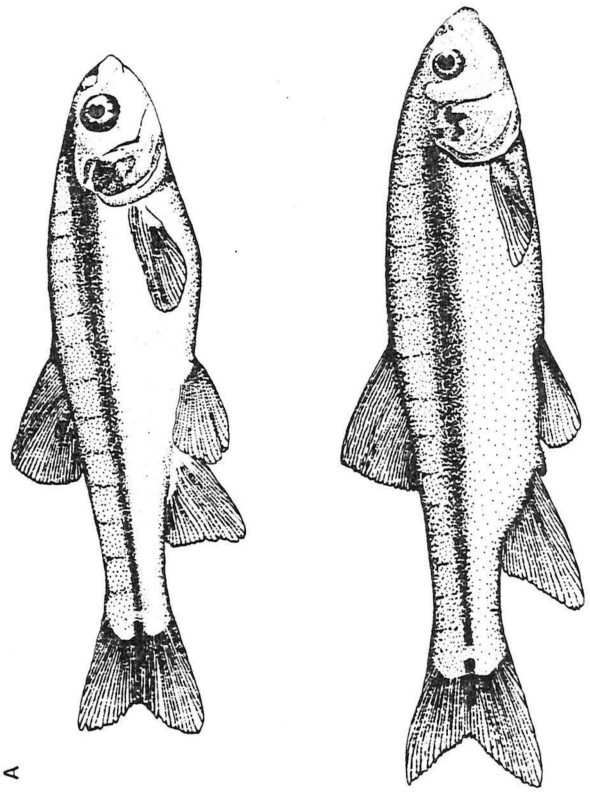

A

Table 1. Measurements (mm) of Agosia chrysogaster from Aravaipa Creek, Arizona (Station 2, 23 April 1978). Means followed by ± one standard deviation.

MEASUREMENT	MALES	FEMALES	MALES + FEMALES
n	13	13	26
Body Weight (g)	2.78 ± 0.30	3.27 ± 0.44	3.03 ± 0.45
Total Length	65.87 ± 2.32	65.77 ± 2.15	65.82 ± 2.19
Standard Length	53.22 ± 2.01	53.42 ± 1.95	53.32 ± 1.94
Length of Head	13.83 ± 0.75	13.60 ± 0.60	13.72 ± 0.67
Depth of Head	9.67 ± 0.46	9.91 ± 0.39	9.79 ± 0.43
Depth of Body	13.60 ± 0.70	14.41 ± 0.63	14.00 ± 0.77
Depth of Caudal Peduncle	5.95 ± 0.22	5.44 ± 0.26	5.70 ± 0.35
Width of Interorbital	4.94 ± 0.22	4.75 ± 0.32	4.85 ± 0.29
Length of Depressed Dorsal Fin	14.14 ± 0.55	11.69 ± 0.55	12.91 ± 1.36
Length of Depressed Anal Fin	11.69 ± 0.50	12.60 ± 0.45	12.14 ± 0.66
Length of Pectoral Fin	10.56 ± 0.60	9.43 ± 0.33	9.99 ± 0.75
Length of Pelvic Fin	10.96 ± 0.67	8.96 ± 0.37	9.96 ± 1.15
Length of Caudal Fin	12.64 ± 0.66	12.35 ± 0.26	12.49 ± 0.51

Table 2. Analysis of variance for significant sexually dimorphic characters in Agosia chrysogaster (n = 26). $F > 7.82$ with 1,24 d.f., $p < 0.01$ (* $p < 0.001$, $F > 14.0$).

CHARACTER	SOURCE OF VARIATION	SUM OF SQUARES	MEAN SQUARE	F VALUE
Length of Depressed Dorsal Fin	Between Sexes	39.07	39.07	129.49*
	Error Factor	7.24	0.30	
	Total	46.31		
Length of Pelvic Fin	Between Sexes	26.08	26.08	88.82*
	Error Factor	7.05	0.29	
	Total	33.13		
Length of Pectoral Fin	Between Sexes	8.33	8.33	35.45*
	Error Factor	5.64	0.24	
	Total	13.97		
Depth of Caudal Peduncle	Between Sexes	1.68	1.68	28.93*
	Error Factor	1.39	0.06	
	Total	3.07		
Length of Depressed Anal Fin	Between Sexes	5.47	5.47	24.27*
	Error Factor	5.41	0.23	
	Total	10.88		
Body Weight	Between Sexes	1.57	1.57	11.04
	Error Factor	3.40	0.14	
	Total	4.97		
Depth of Body	Between Sexes	4.29	4.29	9.65
	Error Factor	10.67	0.44	
	Total	14.96		

When each significant character was further tested in discriminant function analysis, Mahalanobis D^2 values followed the same ranking as ANOVA F-scores (Table 3). Length of depressed dorsal fin was the only character that had no segregation errors in 26 cases, thus providing the highest D^2 value and associated probability (AP) of complete segregation, 129.49 and 98.87%, respectively. Body weight (D^2 = 11.04, AP = 72.26%) and depth (D^2 = 9.65, AP = 70.57%) were lowest.

Although length of depressed dorsal and pelvic fins appear the best dimorphic characters for determining sex in A. chrysogaster, their combination (D^2 = 131.24, AP = 98.89%) resulted in no better ability to segregate specimens by sex than the first alone. On the contrary, other combinations, i.e. length of depressed dorsal fin with depressed anal fin and length of pelvic fin with depressed anal fin (Table 4), resulted in higher D^2 values and AP of segregtaion (D^2 = 260.91, AP = 100% and D^2 = 156.19, AP = 99.77%, respectively). Groupings above a single pair, e.g. length of depressed dorsal fin with pelvic fin with depressed anal fin (D^2 = 261.20, AP 100%), generally offered little new information in differentiating specimens by sex.

Tuberculation occurs in both sexes, but only 12 of 780 females (approximately 1.5%) exhibited the phenomenon. Tuberculate females averaged 78.6 $\pm$ 8.3 mm TL (64.94 $\pm$ 7.17 mm SL) and were only found during spring/summer (May through August) and autumn (September and October) breeding periods. Tubercles in females were poorly developed and restricted to the dorsum of the head from occiput to nostrils.

Table 3. Discriminant function analysis of significant ($p < 0.01$) sexually dimorphic characters in Agosia chrysogaster ($n = 26$).

MEASUREMENT	SEGREGATION ERRORS/26 CASES	MAHALANOBIS D^2 VALUE	ASSOCIATED PROBABILITY (%)
Length of Depressed Dorsal Fin	0/26	129.49	98.87
Length of Pelvic Fin	2/26	88.82	95.25
Length of Pectoral Fin	4/26	35.45	88.75
Depth of Caudal Peduncle	3/26	28.93	87.01
Length of Depressed Anal Fin	6/26	24.27	82.42
Body Weight	7/26	11.04	72.26
Depth of Body	8/26	9.65	70.57

Table 4. Discriminant function analysis of paired morphometric characters of Agosia chrysogaster (Mahalanobis D^2 value above, % Associated Probability below).

	Length of Depressed Dorsal Fin	Length of Pelvic Fin	Length of Pectoral Fin	Depth of Caudal Peduncle	Length of Depressed Anal Fin
Length of Depressed Dorsal Fin	---				
Length of Pelvic Fin	131.24 98.89	---			
Length of Pectoral Fin	143.38 99.34	123.01 99.22	---		
Depth of Caudal Peduncle	133.28 99.29	98.63 95.91	49.96 91.35	---	
Length of Depressed Anal Fin	260.91 100	156.19 99.77	131.38 98.82	81.88 95.75	---

Occasional tubercles occurred on the opercles, but none was present on the preopercles.

Adult males were in tuberculate condition, particularly on the head and opercles, throughout the year. Immature males were nontuberculate. A description of typical tubercle distribution in breeding males follows:

Head and opercles - tubercles first appear on dorsum of head, developing into profuse, scattered pattern; heavy tuberculation extends from occiput onto snout to point anterior and medial to nostrils; tubercles encircle orbit, except anteriorly, particularly concentrated along supraorbital ridge; heavy tuberculation covers surface of opercles; preopercles only sparsely tuberculate. Body - small tubercles extend posteriad along dorsal midline from occiput to origin dorsal fin and along dorsal midline of caudal peduncle to procurrent rays of caudal fin. Caudal peduncle - small tubercles in regular rows on lateral surfaces of caudal peduncle, one per scale; ventral surface caudal peduncle with tubercles extending anteriorly from procurrent rays to posterior base anal fin. Pectoral fin - tubercles in double row along dorsal surface first pectoral ray, extending from origin of ray to distal end. Pelvic fin - tubercles in single row on first through sixth rays, beginning near origin of rays, extending over each dorsal surface, but never reaching distal tips. Dorsal fin - tubercles in single row over proximal half first ray margin, beginning near origin; one or more tubercles infrequently on either lateral surface of first through sixth rays. Anal fin - tubercles in single rows on lateral surfaces second through sixth

rays; tubercles medially over fin, not extending to origin of rays nor distally to tips. Caudal fin - tubercles last appear on caudal fin; in highly developed males, tubercles as single rows on each ray, developing over lateral surfaces of proximal half beginning at base.

All tubercles are sharp-pointed, and depending on degree of proliferation and development, rugose to touch. Largest tubercles are on the dorsum of the head and lateral surfaces of the opercles. Smallest are along the dorsal midline and over lateral and ventral surfaces of the caudal peduncle. Tubercles on paired and unpaired fins are intermediate in size between extremes.

Tuberculation in A. chrysogaster, as in most cyprinoids, is most profuse during spawning peaks and therefore is probably under hormonal control (Ramaswami and Hasler 1955). Koehn (1965) reported head tubercles in male red shiner (Notropis lutrensis) serving an important function in breeding behavior of that species by stimulating the female to spawn. Reighard (1903, 1904) implied that heavy tuberculation on sides of the body and fins assist a male in lateral contact with a female during emission of gametes. Nuptial tubercles, and the expanded fins of males of A. chrysogaster, may aid them in maintaining close contact as they flank females that enter nesting areas (see below).

Spawning Behavior

Spawning behavior of A. chrysogaster has been described by Minckley 1969, 1973, Minckley and Barber 1971, and Lewis 1978b. The account by Minckley (1973) was as follows:

> "Tuberculate males move randomly, back-and-forth over the nest areas, without any obvious territoriality. Females enter the area singly. She is immediately flanked by 1 to 4 males and is followed closely as she appears simply to wander through the area. One, or rarely two, males position themselves postero-laterally to the female. She then dips into a depression, closely followed by the male(s), and a flurry of sand obscures what must be the actual spawning act. The fish then lie quietly for a second,then move rapidly away, the males to resume their patrolling, and the female out of the area, usually into deeper waters."

My personal observations of spawning behavior agree with his report.

Table 5 summarizes information from Aravaipa Creek regarding nesting areas and reproductive products recovered from a limited number of nests. Nesting areas were within or at the mouths of stream-connected backwaters where little (0.07 $\pm$ 0.04 m/s) or no current existed. They were infrequently on shallow, laminar, sand-bottomed runs. Nests are saucer-shaped depressions in shallow (< 18 cm) open areas that are clear of diatoms, detritus, and plant debris. They averaged 13.5 $\pm$ 2.6 cm in diameter and were excavated 2.3 $\pm$ 0.8 cm deep with a 1.2 $\pm$ 0.2 cm margin raised above surrounding substrate. Nest substrate varied in size from fine sand (0.063 mm diameter) to coarse gravel (31 mm). Number of nests per square meter (m^2) ranged from 1 to 50 and averaged 21.3 $\pm$ 11.9. Water over nesting sites was generally not circulating with cooler water of the mainstream and was often more than 1.0^0 C warmer. Water temperatures over nesting areas averaged 23.4 $\pm$ 3.2^0 C (limits 16.8 to 29.7^o C).

Non-adhesive, fertilized eggs were retrieved from nests by agitating bottoms and sides of depressions and collecting reproductive products with a fine-mesh (< 2.0 mm) aquarium net. All ova were removed from nests

Table 5. Nest location, description, and reproductive product characteristics of Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.

CHARACTER	SAMPLE SIZE	MEAN	STANDARD DEVIATION	RANGE
Nest location	connected backwaters and runs free of algae and organic debris			
Nest diameter (cm)	106	13.5	2.6	7.5 - 20
Nest depth (cm)	106	2.3	0.8	1.0 - 4.6
Height of nest margin above surrounding substrate (cm)	18	1.2	0.2	0.9 - 1.7
Water depth (cm)	149	8.5	4.0	2.9 - 17.9
Water temperature ($^{\circ}$ C)	16	23.4	3.2	16.8 - 29.7
Current (m/s)	6	0.07	0.04	0.04- 0.13
Substrate	fine sand to coarse gravel (0.063 - 31 mm diameter)			
Nests/m^2	12	21.3	11.9	8 - 50
Ova/nest	2	16.0	5.7	12 - 20
Ova diameter (mm)	32	2.3	0.2	1.95- 2.7
Ova weight (mg)	32	5.3	0.8	3.9 - 6.5
Size (TL) @ hatching (mm)	100	6.44	0.33	6.01- 6.87

on two occasions, resulting in an average of 16 ± 5.7 ova per nest. Preserved ova from both collections averaged 2.3 ± 0.2 mm in diameter and 5.3 ± 0.8 mg (n = 32).

Nests were observed throughout much of the year, with highest concentrations in spring and late summer. Young hatch in less than four days at water temperatures above 24° C (Minckley and Barber 1971). Young (as characterized by Winn and Miller 1954) were first observed in March and averaged 6.44 ± 0.33 mm TL at hatching (n = 100). They remained within nest depressions until yolk sacs were absorbed, then dispersed into backwaters. Minckley (1973) and Lewis (1978b) reported rapid growth in longfin dace, with attainment of sexual maturity within a year of hatching (31.6 to 44.5 mm SL). Females in Aravaipa Creek first produced Class I and II ova at 42.1 mm SL.

Collections from both stations resulted in a sex ratio of 1.1 females to 1.0 males in pooled samples (n = 1,491). This does not differ significantly ($p > 0.05$) from a 1:1 ratio and therefore detects no selective advantage based on sex.

Spawning Periodicity

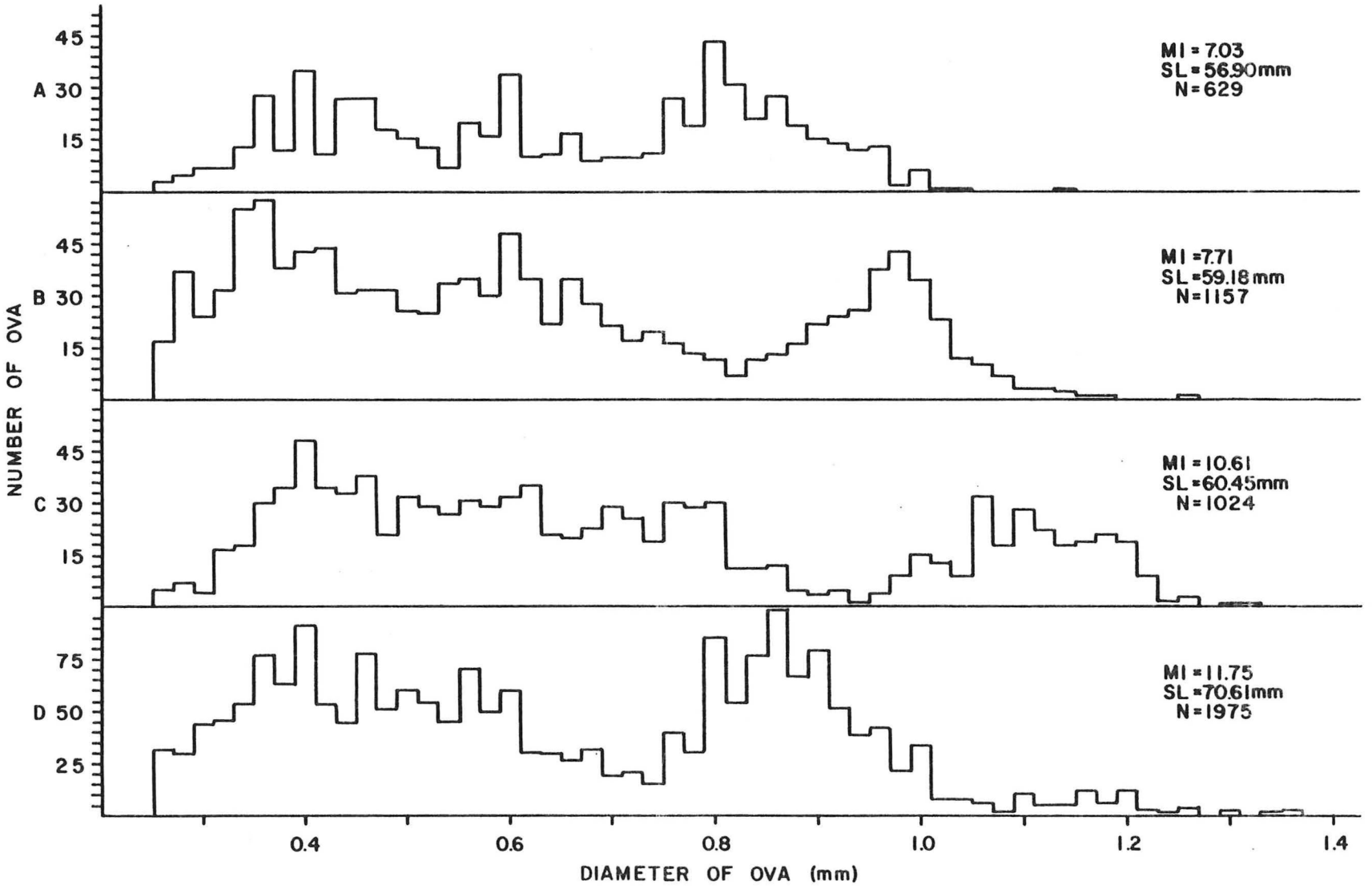
At least three distinct classes of ova (I-III) were in the mature ovary of a female A. chrysogaster. Egg classes were intermixed throughout the lumen, with no visible segregation other than a restriction of primary oocytes (< 0.2 mm diameter) to the peripheral, germinal epithelium. Those females with Class I ova free of mesovarian tissue concentrated them ventroposteriorly near the oviduct. Atretic ova, identified by their dark granular appearance and ease of disintegration upon contact, were rarely observed in spent

females. Because atretic ova were undergoing a process of resorption, and were an insignificant proportion of total intraovarian ova, no attempt was made to measure or count them.

Four females in various stages of development, i.e. developing, mature, and spent, were selected from the September sample to demonstrate segregation and development of ova classes. Prerecruitment (Class III) and recruitment (Class II) cohorts segregate and develop towards Class I ova until they reach maturity (Fig. 4A-C). Spent females resume withdrawing ova as distinct cohorts from the general ova stock, although mature eggs may be residual after completion of spawning (Fig. 4D).

Clear separation between recruitment cohorts and a mature cohort is indicative of definite spawning periodicity (Hickling and Rutenberg 1936). A lack of modal distinction is representative of an indefinite process, wherein eggs are withdrawn to undergo maturation on a continual basis rather than in distinct groups. Withdrawal of at least two complements of ova for maturation in A. chrysogaster suggests an individually bi- or multimodal spawning period, a period consisting of successive cohorts of Class I and II ova from the available pool of prerecruitment (Class III) eggs. The first complement of Class III ova is segregated from the germinal epithelium as a single, large cohort during post-reproductive periods of October and November. As the ovaries begin a maturation process (vitellogenesis) in December and January, a portion of the Class III cohort is developed into Class II ova. A general depletion of Class III ova and an increase in the ratio of Class II to Class III ova per

Figure 4. Ova development in four selected females of Agosia chrysogaster from Aravaipa Creek, Arizona (September 1977). Females are within various stages of development, i.e. developing (A, B), mature (C), and spent (D).


NUMBER OF OVA
A
B
C
D
45
30
15
75
50
25
MI = 7.03
SL = 56.90mm
N = 629
MI = 7.71
SL = 59.18mm
N = 1157
MI = 10.61
SL = 60.45mm
N = 1024
MI = 11.75
SL = 70.61mm
N = 1975
0.4
0.6
0.8
1.0
1.2
1.4
DIAMETER OF OVA (mm)

cm SL (expressed as %) may be seen between February and March (Table 6). Major spawning appears to occur in spring when approximately 87% of the Class II ova disappear from the ovary. The remaining Class II ova are either resorbed, which was not observed, or are held and developed through the summer. Few Class I ova were ever found in ovaries, which implies that development from Class II to Class I is rapid, and of small clutch-size. As noted below, large numbers of Class I ova (n = 80) were found only in two instances. Individual females typically contained less than 10 Class I ova. Females must therefore produce only a few ripe eggs periodically throughout the spawning season, which corresponds generally to the low numbers of eggs found in individual nests (Table 5). All Class I ova apparently are spawned; only a few atretic ova were observed.

A second complement of Class III ova is segregated from germinal epithelium during May through July, and supplements the residual Class III ova from the first complement. Part of this combined prerecruitment cohort is developed through Class II ova in August and shed as Class I eggs in September. The low ratio of Class II to Class III ova per cm SL in late spring and summer (May and July) confirms formation of a second ova complement (Table 6). The ratio of Class II to Class III ova is increased in September as prerecruitment ova are advanced to maturity. All Class II ova that mature into Class I eggs are again spawned. A residual complement of Class II remains with the female, to be retained through winter for availability the following spring, or possibly to be resorbed.

Table 6. Mean Class I, II, and III egg counts for Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona. Mean followed by ± one standard deviation.

DATE	n	Class III Ova	Class II Ova	Class I Ova	Class III Ova / cm SL	Class II Ova / cm SL	Class II/cm SL / Class III/cm SL X 100
November	5	2,225.2 ± 615.7	8.2 ± 18.3	0	402.9 ± 107.4	1.5 ± 3.4	0.5
January	3	2,279.0 ± 484.4	257.3 ± 48.5	0	435.7 ± 111.4	49.0 ± 10.1	11.4
February	3	2,568.7 ± 674.4	321.7 ± 82.8	48.0 ± 77.9	445.0 ± 72.6	55.8 ± 9.1	12.5
March	3	2,229.0 ± 1,441.9	353.0 ± 284.5	1.3 ± 1.5	404.4 ± 166.2	61.7 ± 38.1	15.7
May	3	1,437.7 ± 474.0	43.7 ± 42.0	0	240.4 ± 74.7	7.3 ± 6.9	2.8
July	3	2,215.3 ± 832.1	35.3 ± 56.9	0	372.4 ± 108.1	6.4 ± 10.3	2.1
September	9	693.9 ± 362.7	224.7 ± 192.5	3.3 ± 6.4	113.3 ± 49.0	35.6 ± 27.8	27.0
October	10	744.8 ± 367.7	54.3 ± 75.1	0.3 ± 0.9	155.9 ± 63.9	10.7 ± 14.2	6.0

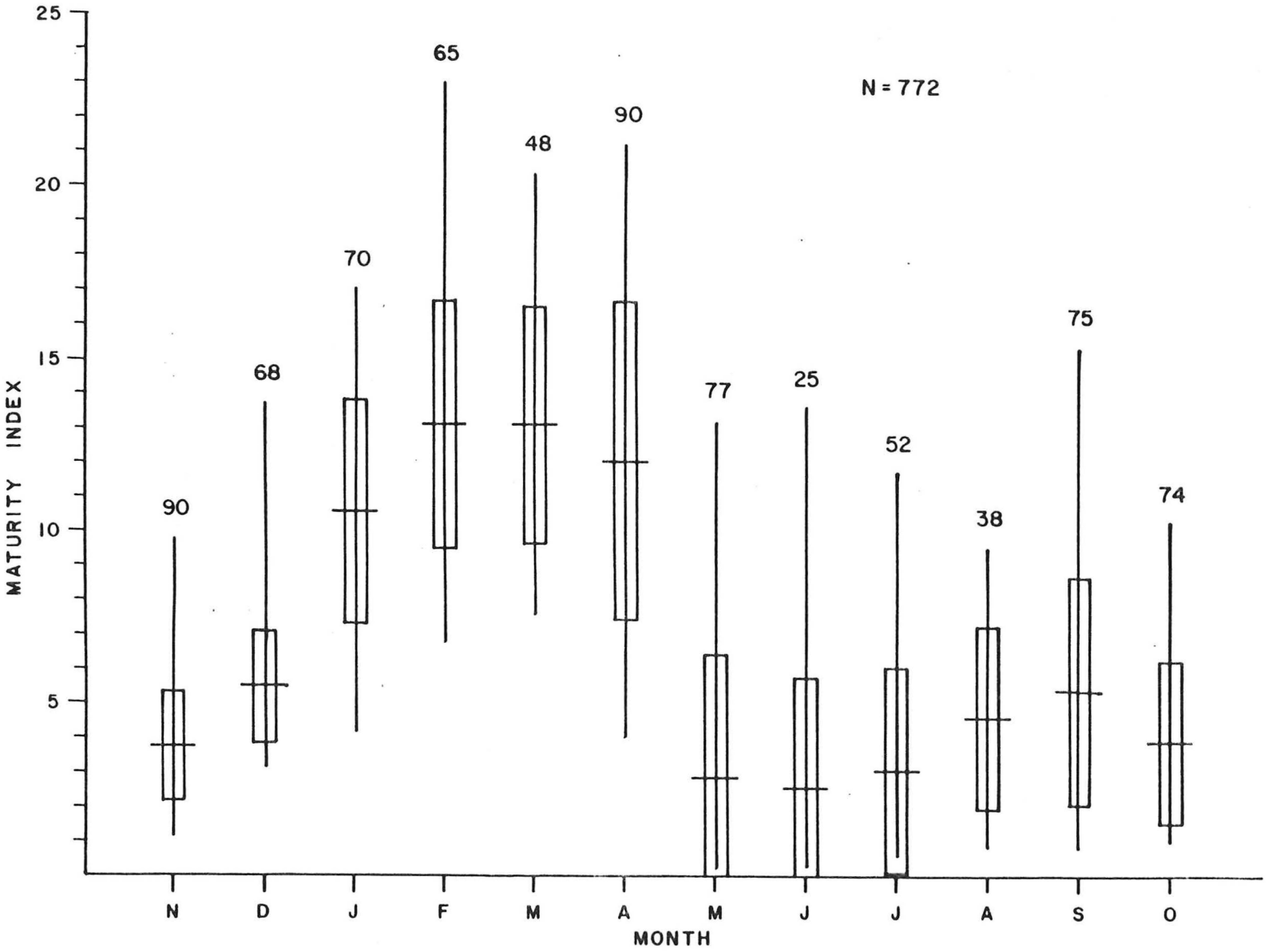
Individual maturity indices (MIs) for female longfin dace varied from a minimum of 0.20% in May to a maximum of 23.09% in February (Table 7). MIs varied widely within each monthly sample (Fig. 5) indicating overlap in individual spawning periods, i.e. asynchronous spawning behavior. Furthermore, females with high MIs (> 9.5) and Class II ova were collected in all sampling periods, indicating that spawning potential was throughout most of the year. On only two occasions, dissected females were found with ripe ova concentrated ventroposteriorly in the ovaries and occupying the oviduct. In the first instance (26 February 1978), 80 ova were counted which averaged 1.26 ± 0.062 mm diameter (limits 1.12 to 1.40 mm). In the second (18 June 1978), 80 ova were also enumerated, but the average size was smaller, 1.18 ± 0.030 mm diameter (limits 1.10 to 1.24 mm). Although ripe ova numbered 80 on both occasions, the average number of fertilized eggs recovered from a given nest was 16 ± 5.7 (Table 5). Eggs must therefore be deposited in more than one nest location and not all shed at once. Apparently, A. chrysogaster females are capable of yolking and holding egg complements until threshold stimuli to spawning are received, thus further complicating determination of individual periodicity.

Although protracted spawning strategies obscure individual periodicity and preclude accurate determination of individual spawning duration and time interval between successive spawns, a species as a whole may exhibit definite periodicity (De Jong 1940). Therefore, although individual spawning activity appears asynchronous in longfin dace, mean MI data suggest that populations in Aravaipa Creek reach

Table 7. Maturity index statistics of Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona (n = 772). Data represent mean ± one standard deviation with ranges in parentheses.

DATE	n	MEAN ± STD. DEV.	DATE	n	MEAN ± STD. DEV.
November	90	3.75 ± 1.52 (1.18 - 9.80)	May	77	2.85 ± 3.41 (0.20 - 13.13)
December	68	5.48 ± 1.54 (3.10 - 13.75)	June	25	2.58 ± 3.06 (0.23 - 13.59)
January	70	10.55 ± 3.11 (4.16 - 17.09)	July	52	3.05 ± 3.02 (0.59 - 11.64)
February	65	13.12 ± 3.47 (6.78 - 23.09)	August	38	4.57 ± 2.53 (0.74 - 9.49)
March	48	13.11 ± 3.30 (7.57 - 20.31)	September	75	5.32 ± 3.17 (0.78 - 15.24)
April	90	12.06 ± 4.41 (3.66 - 21.39)	October	74	3.85 ± 2.27 (0.98 - 10.28)

Figure 5. Mean maturity indices of 772 Agosia chrysogaster ± one standard deviation on either side of mean (box), 1977-78, Aravaipa Creek, Arizona. Vertical bars represent the range with the number of observations indicated above.

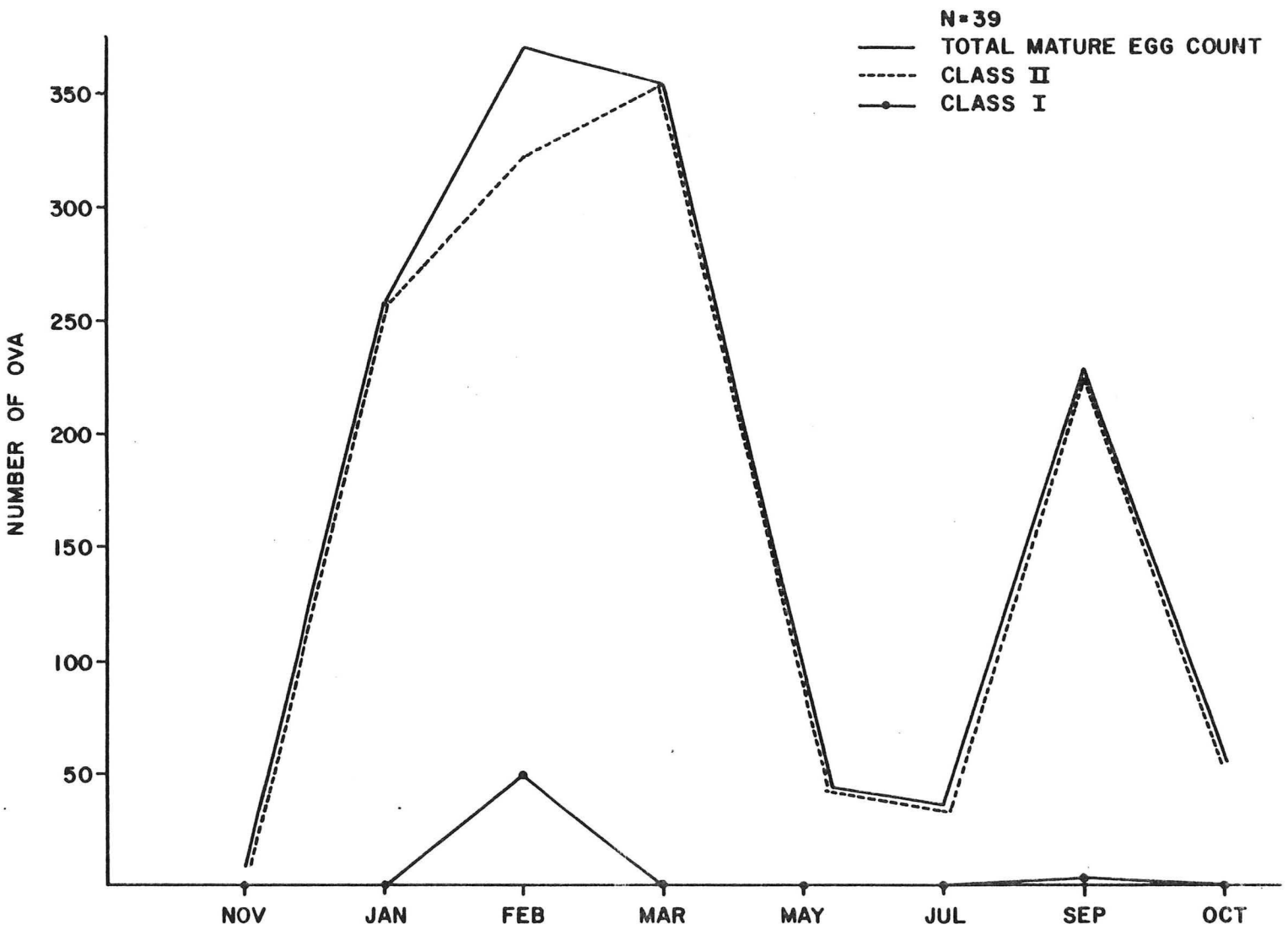

N = 772
MATURITY INDEX
25
20
15
10
5
90
68
70
65
48
90
77
25
52
38
75
74
N
D
J
F
M
A
M
J
J
A
S
O
MONTH

peak spawning condition semiannually. Ovaries develop through winter until reaching peak reproductive condition in February. The mean MI for females collected during that period was 13.12%, n = 65 (Table 7). Spawning continued through April, subsided by May, and lowest mean MI was in June (2.58%, n = 25). Ovaries in that period contained primarily Class III ova. A gradual increase in MI in late summer culminated in a minor spawning peak by September (mean MI 5.32%, n = 75), followed by another marked decline in reproductive activity. Duration of the second peak was short compared to the first (Fig. 5). Variation in individual maturity indices was greatest during spawning peaks, due to the presence of spent females in the population.

Another approach to explore spawning periodicity was to plot primary fecundity (number of ripe ova, i.e. Class I), secondary fecundity (number of maturing ova, i.e. Class II) and total fecundity (Classes I and II) over time (Fig. 6). Class I ova were present in only four periods, i.e. February, March, September, and October, during the spring and late summer spawning peaks. They were most numerous in February and essentially absent in October. Total fecundity corresponded to the bimodal curve of maturity indices in Figure 5, reconfirming a semiannual spawning nature of the longfin dace population in Aravaipa Creek.

Spawning periodicity differed in up- and downstream populations (Station 1 versus Station 2). Fish from Station 2 reached peak reproductive condition two months prior to those at Station 1 in spring (Fig. 7). Spawning was synchronous in both populations by May and each exhibited a secondary peak in September followed by a decline

Figure 6. Mean primary, secondary, and total fecundity of Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.


N=39
TOTAL MATURE EGG COUNT
CLASS II
CLASS I
NUMBER OF OVA
350
300
250
200
150
100
50
NOV
JAN
FEB
MAR
MAY
JUL
SEP
OCT

in reproductive activity in October. These observations were tested by Student t-test for each sample period. Maturity indices differed significantly ($p < 0.05$) during winter and spring months, but not during summer and autumn (Table 8). Differences, other than elevation, between the two stations include a general lack of cover at Station 2 resulting in increased solar radiation over the streambed and presumably warmer water temperatures. Additionally, Station 2 is influenced by a higher incidence of flooding due to its downstream location, which may induce females to spawn earlier than at Station 1 (see later).

Fecundity

Most authors describe fecundity as the number of eggs produced prior to spawning and distinguish it from fertility based on whether or not the eggs were shed. Fecundity of an individual female varies with age, size, and condition. Fecundity definitions for A. chrysogaster follow those described by Espinosa (1968), i.e. primary, secondary, and total. Primary Fecundity is the number of ripe ova (Class I) produced, whereas Secondary Fecundity includes the total number of maturing ova (Class II). Total Fecundity is defined as the total number of mature ova greater than or equal to 0.8 mm in diameter (Classes I and II combined). The last index of fecundity considered during the present study was Relative Fecundity, i.e. the number of eggs per unit weight or length of the fish (Nikolsky 1963).

Mean primary fecundities for A. chrysogaster ranged from 0 to 48 ova. Class I ova were present only during the spring and late summer spawning peaks with a majority of ripe ova appearing in February

Figure 7. Mean maturity indices for upstream (Station 1, elevation 946 m, n = 372) and downstream (Station 2, elevatin 704 m, n = 400) populations of Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.

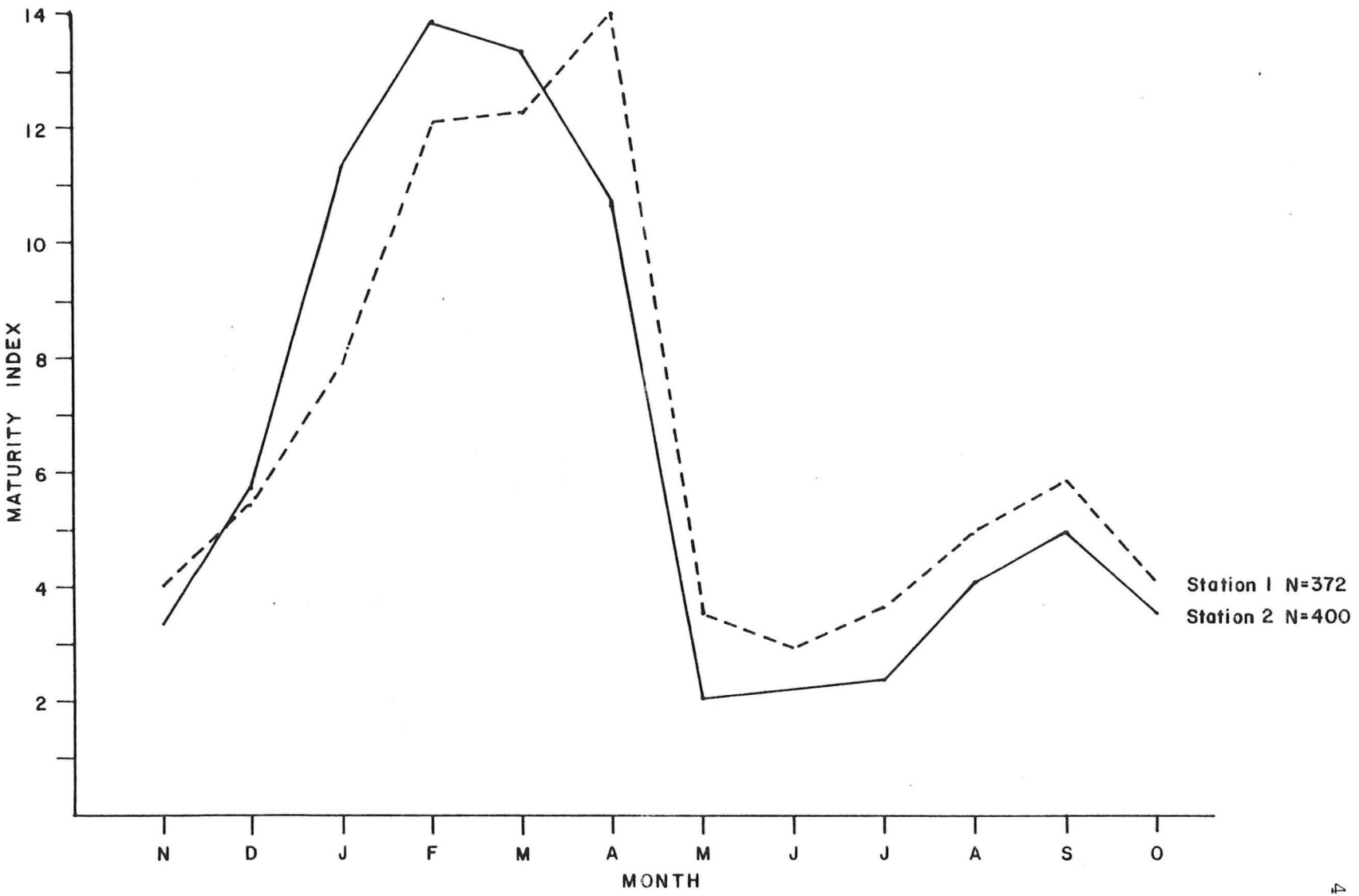

14
12
10
8
6
4
2
MATURITY INDEX
N
D
J
F
M
A
M
J
J
A
S
O
MONTH
Station 1 N=372
Station 2 N=400

Table 8. Maturity index statistics for upstream (Station 1, elevation 946 m, n = 372) and downstream (Station 2, elevation 704 m, n = 400) populations of Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona (* denotes significantly different (t-test; $p < 0.05$) mean maturity indices between stations).

DATE	STATION	n	MEAN ± STD. DEV.	DATE	STATION	n	MEAN ± STD. DEV.
November*	1	54	4.01 ± 1.61 (2.05 - 9.80)	May*	1	40	3.58 ± 3.87 (0.26 - 13.13)
	2	36	3.37 ± 1.31 (1.18 - 8.03)		2	37	2.06 ± 2.68 (0.20 - 12.89)
December	1	55	5.42 ± 1.12 (3.36 - 8.64)	June	1	12	2.95 ± 3.85 (0.23 - 13.59)
	2	13	5.73 ± 2.73 (3.10 - 13.75)		2	13	2.25 ± 2.22 (0.53 - 7.92)
January*	1	16	7.92 ± 2.35 (4.16 - 12.04)	July	1	28	3.63 ± 3.42 (0.59 - 11.64)
	2	54	11.33 ± 2.88 (5.17 - 17.09)		2	24	2.38 ± 2.37 (0.72 - 8.02)
February*	1	27	12.10 ± 2.64 (6.78 - 18.43)	August	1	21	4.96 ± 2.77 (0.74 - 9.49)
	2	38	13.84 ± 3.84 (7.20 - 23.09)		2	17	4.09 ± 2.20 (1.06 - 7.78)
March	1	11	12.25 ± 2.83 (8.53 - 17.02)	September	1	30	5.85 ± 2.67 (1.50 - 11.83)
	2	37	13.37 ± 3.42 (7.57 - 20.31)		2	45	4.97 ± 3.44 (0.78 - 15.24)
April*	1	37	14.00 ± 3.50 (6.74 - 20.65)	October	1	41	4.08 ± 2.09 (1.22 - 8.14)
	2	53	10.71 ± 4.51 (3.66 - 21.39)		2	33	3.56 ± 2.48 (0.98 - 10.28)

(Table 9, Fig. 6). Mean secondary fecundities ranged from 8.2 to 353 ova throughout the year. Total fecundity ranged from 8.2 to 369.7 ova.

The high variability associated with fecundity statistics is attributable to asynchronous spawning behavior of the individual, semiannual spawning periodicity of the population, and the protracted spawning season.

Simple linear regression analysis ($Y = a + bX$, where "a" is the Y-intercept and "b" the regression coefficient) was employed to relate total fecundity (dependent variable "Y") to fish length (TL and SL), weight, ovary weight, and maturity index (independent variables "X"). Data from eight monthly collections ($n = 41$) were combined to estimate fecundity for A. chrysogaster (Table 10, Figs. 8-12).

Generally, it is unjustifiable to extrapolate from regression equations beyond observed values of the independent variable X unless it is "believed" that the described function holds for X value outside the range of those observed, i.e. remains linear (Zar 1974). Therefore, the best predictive value for dependent variable Y occurs between the following values for X: 53.07 to 83.31 mm TL, 42.43 to 70.61 mm SL, 1.24 to 6.70 g body weight, 0.0610 to 0.7870 g ovary weight, and 2.62 to 13.96% MI. Relative fecundity estimates (within observed limits) computed from regression equations are as follows: 10.7 ova/mm increase in TL, 12 ova/mm increase in SL, 7.7 ova/0.1 g increase in body weight, 1.0 ovum/mg increase in ovary weight, and 36.9 ova/1% increase in MI.

Table 9. Fecundity statistics for Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona. Means followed by ± one standard deviation.

Date	n	Total Length (mm)	Standard Length (mm)	Body Weight (g)	Ovary Weight (g)	Maturity Index	Primary Fecundity	Secondary Fecundity	Total Fecundity
November	5	67.46 ± 2.88	55.21 ± 2.48	3.0 ± 0.28	0.1177 ± 0.0341	3.92 ± 1.01	0	8.2 ± 18.3	8.2 ± 18.3
January	3	64.68 ± 4.41	52.81 ± 3.81	2.76 ± 0.49	0.2727 ± 0.0653	9.92 ± 1.78	0	257.3 ± 48.5	257.3 ± 48.5
February	3	69.85 ± 7.92	57.27 ± 6.84	3.54 ± 1.52	0.4620 ± 0.1951	13.14 ± 0.81	48 ± 77.9	321.7 ± 82.8	369.7 ± 160.2
March	3	64.01 ± 14.52	52.23 ± 12.53	2.82 ± 2.13	0.3657 ± 0.2731	13.05 ± 0.35	1.3 ± 1.5	353 ±284.5	354.3 ± 285.7
May	3	72.47 ± 1.63	59.54 ± 1.41	4.58 ± 0.12	0.1282 ± 0.0355	2.78 ± 0.72	0	43.7 ± 42	43.7 ± 42
July	3	71.37 ± 5.38	58.59 ± 4.64	3.77 ± 0.88	0.1295 ± 0.0332	3.56 ± 1.29	0	35.3 ± 56.9	35.3 ± 56.9
September	9	70.64 ± 9.60	58.48 ± 8.60	3.82 ± 1.57	0.2860 ± 0.2207	6.57 ± 3.23	3.3 ± 6.4	224.7 ± 192.5	228 ± 196.7
October	10	58.04 ± 4.80	46.53 ± 4.29	1.85 ± 0.57	0.1041 ± 0.0783	5.09 ± 2.60	0.3 ± 0.9	54.3 ± 75.1	54.6 ± 75.3

Table 10. Summary information for linear regression analysis of total fecundity (Y) relative to Agosia chrysogaster length (total and standard), weight, ovary weight, and maturity index (independent variables X), 1977-78, Aravaipa Creek, Arizona.

Character	Regression Equation	n	p	$r_{critical}$	r	$F_{critical}$	F	$t_{critical}$	t
Total Length	Y = -564.698 + 10.659X	41	0.001	0.495	0.504	12.7	13.3	3.558	3.641
Standard Length	Y = -507.603 + 11.986X	41	0.001	0.495	0.509	12.7	13.7	3.558	3.696
Body Weight	Y = - 94.739 + 77.469X	41	0.001	0.495	0.574	12.7	19.1	3.558	4.372
Ovary Weight	Y = - 58.200 + 969.980X	41	0.001	0.495	0.964	12.7	506.7	3.558	22.511
Maturity Index	Y = - 95.956 + 36.936X	41	0.001	0.495	0.805	12.7	72.0	3.558	8.484

Figure 8. Comparison of total fecundity to total length (mm) of 41 Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.

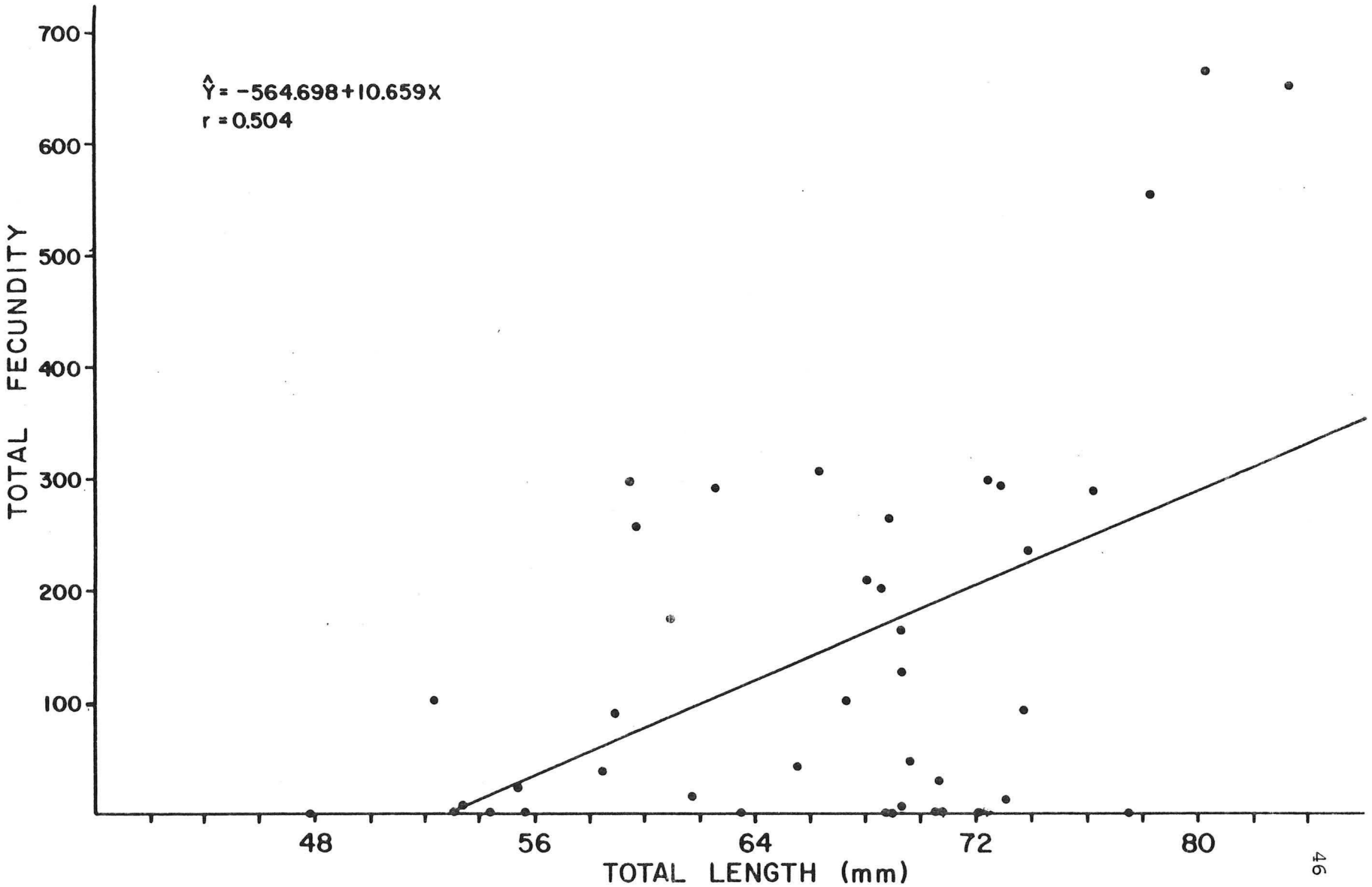

$\hat{Y} = -564.698 + 10.659X$
r = 0.504
TOTAL FECUNDITY
700
600
500
400
300
200
100
48
56
64
72
80
TOTAL LENGTH (mm)

Figure 9. Comparison of total fecundity to standard length (mm) of 41 Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.

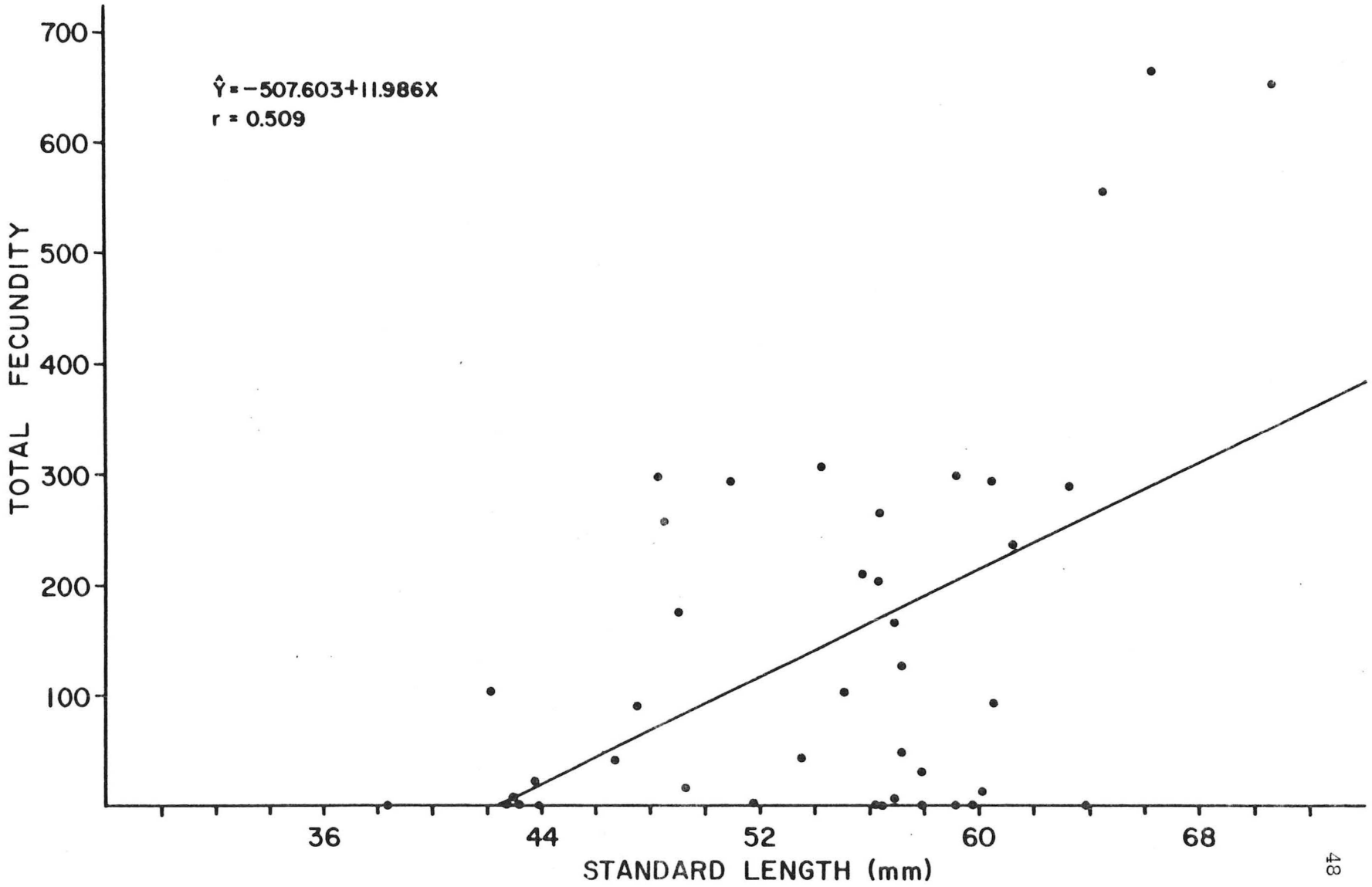

$\hat{Y} = -507.603 + 11.986X$
r = 0.509
TOTAL FECUNDITY
700
600
500
400
300
200
100
36
44
52
60
68
STANDARD LENGTH (mm)

Figure 10. Comparison of total fecundity to fish weight (g) of 41 Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.

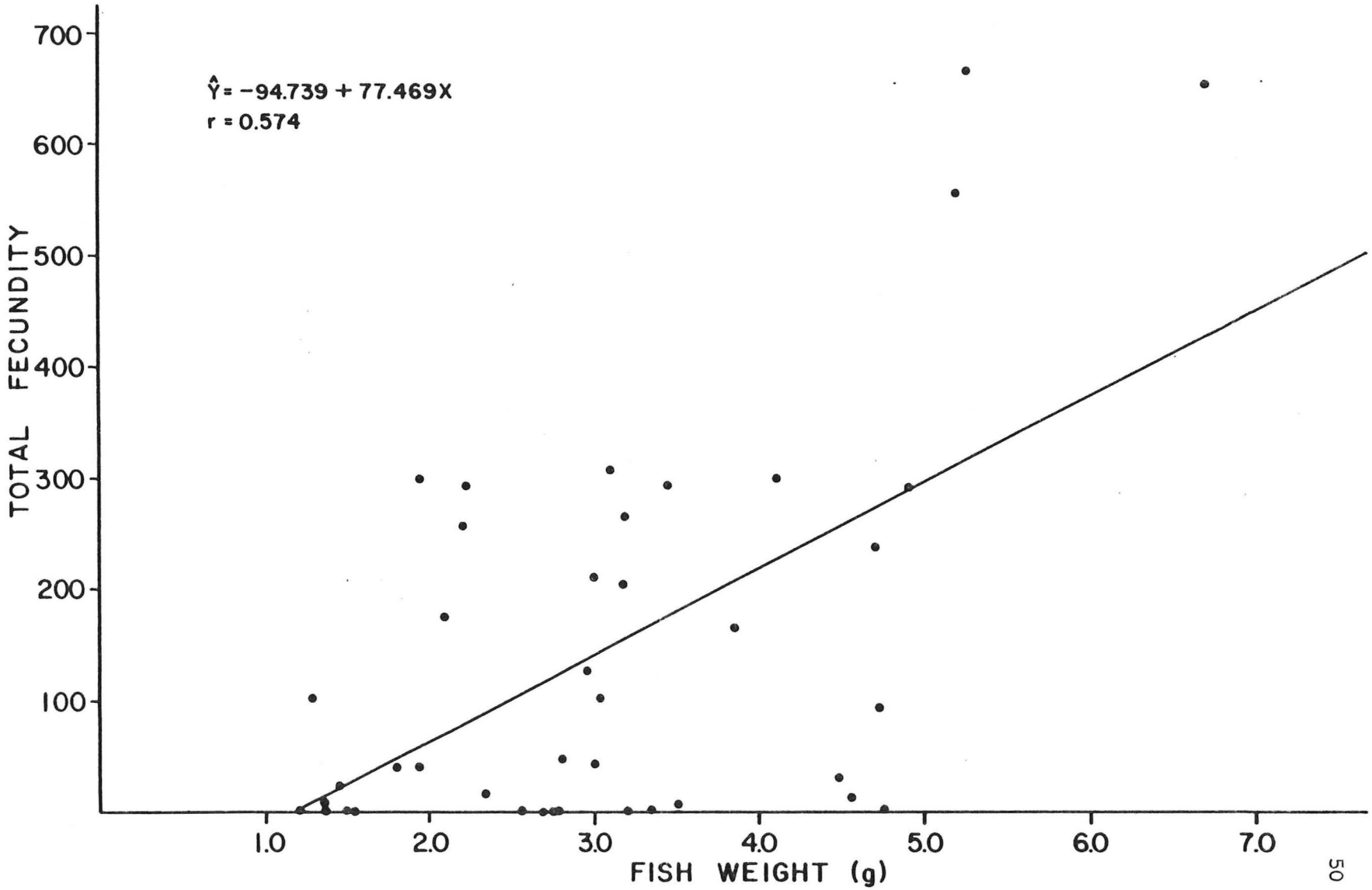

$\hat{Y}$ = −94.739 + 77.469X
r = 0.574
TOTAL FECUNDITY
700
600
500
400
300
200
100
1.0
2.0
3.0
4.0
5.0
6.0
7.0
FISH WEIGHT (g)

Figure 11. Comparison of total fecundity to ovary weight (g) of 41 Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.

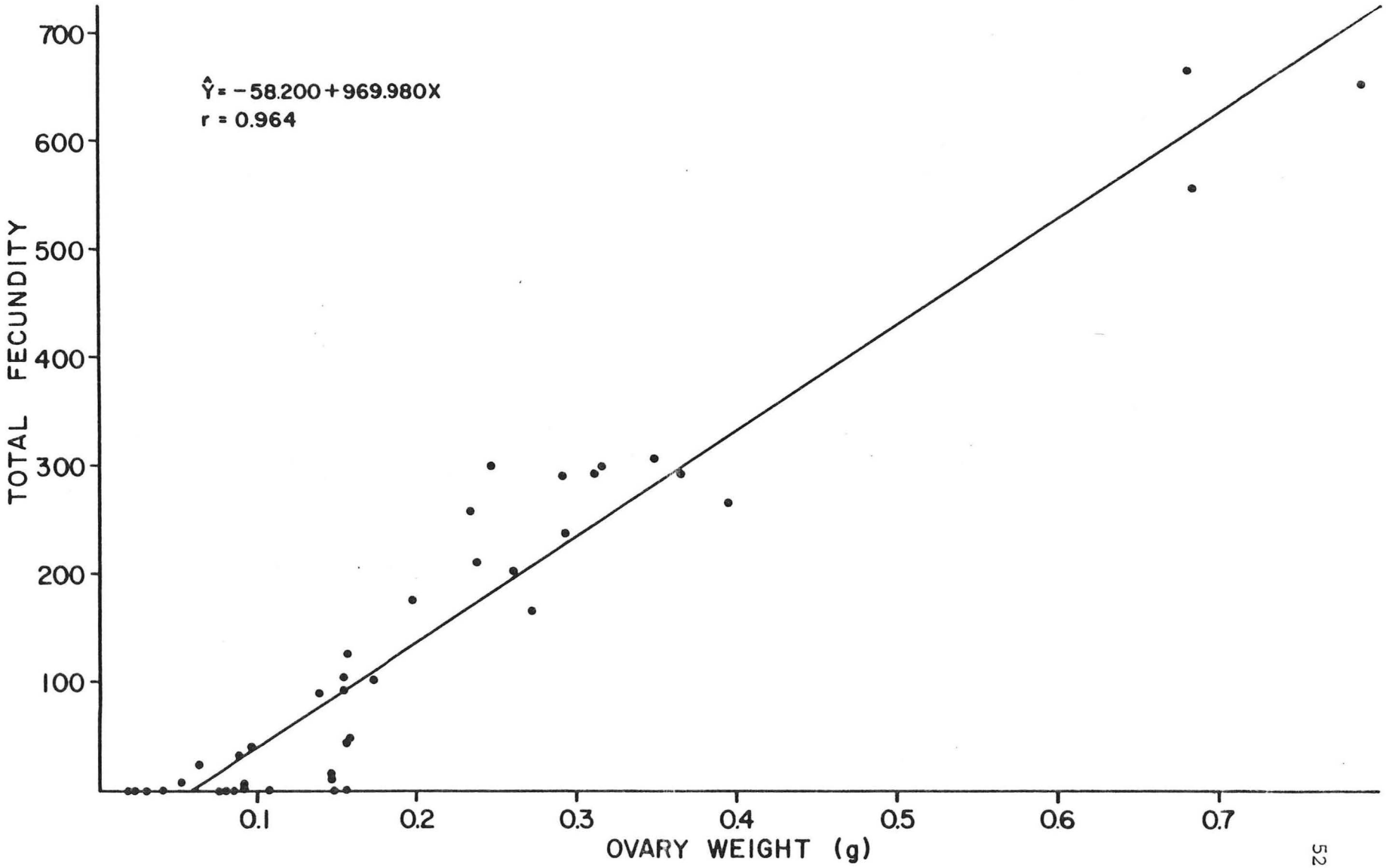
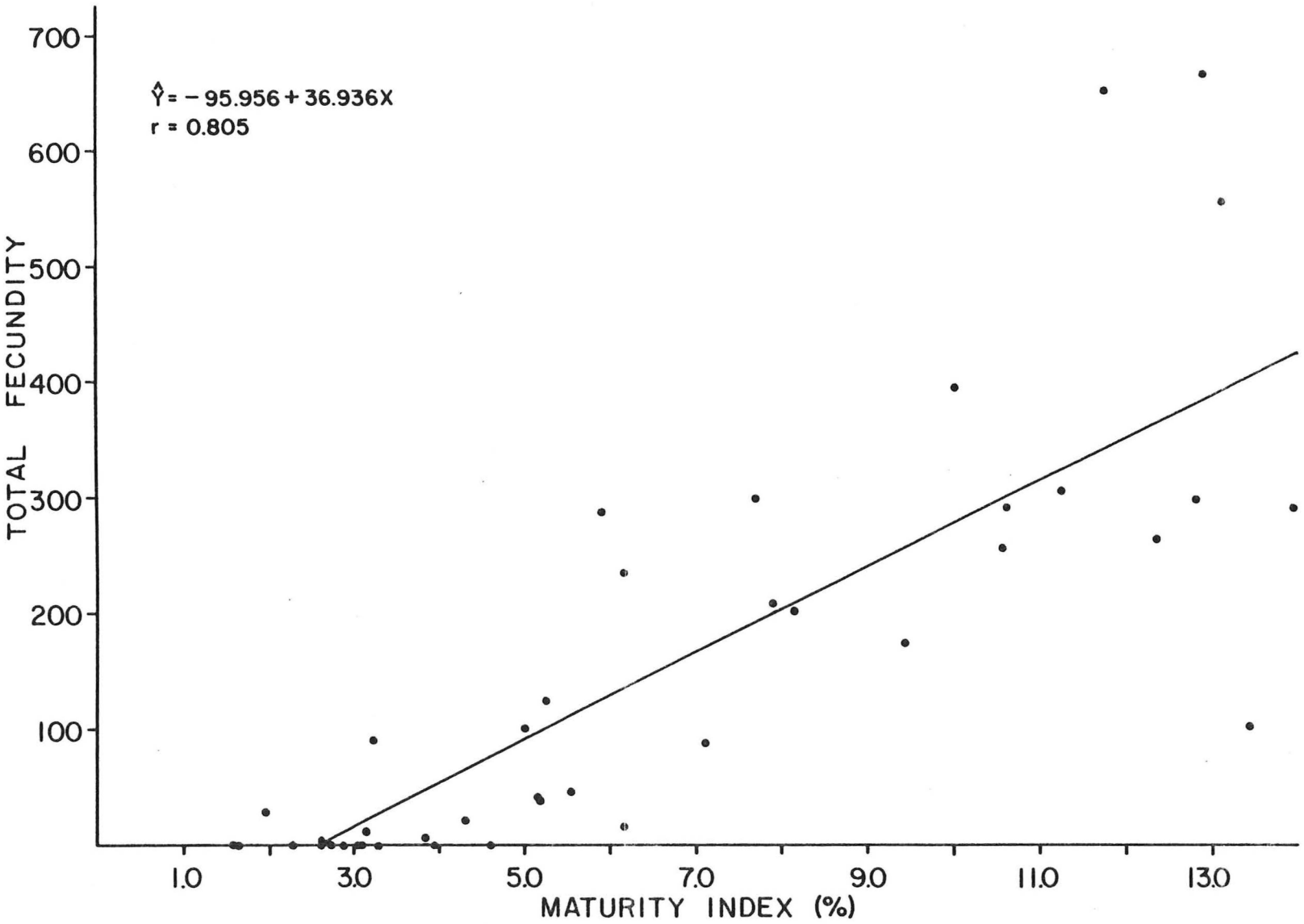

$\hat{Y} = -58.200 + 969.980X$
r = 0.964
TOTAL FECUNDITY
700
600
500
400
300
200
100
0.1
0.2
0.3
0.4
0.5
0.6
0.7
OVARY WEIGHT (g)

Figure 12. Comparison of total fecundity to maturity index of (%) of 41 Agosia chrysogaster, 1977-78, Aravaipa Creek, Arizona.


$\hat{Y} = -95.956 + 36.936X$
r = 0.805
TOTAL FECUNDITY
700
600
500
400
300
200
100
1.0
3.0
5.0
7.0
9.0
11.0
13.0
MATURITY INDEX (%)

The association between variables X and Y was tested using analysis of variance F and Student's t statistics (Table 10). All independent variables (TL, SL, body weight, ovary weight, and MI) were significantly ($p < 0.001$) related to total fecundity. Ovary weight was the best indicator of fecundity in all cases and TL the least reliable. MI was the second most important variable relative to estimating fecundity, followed by body weight. All variables were positively correlated ($r > 0$) to fecundity (Table 10) indicating that the number of mature ova produced increases with corresponding increases in length, weight, ovary weight, and MI. Although fish length is generally considered the preferred variable for relative fecundity computations (Bagenal 1966, 1978), fish length (TL and SL) in A. chrysogaster was the most weakly correlated of the five variables considered ($r < 0.51$). Ovary weight was the most highly correlated variable ($r = 0.964$) and therefore the most reliable indicator of total fecundity.

DISCUSSION AND CONCLUSIONS

Analysis of maturity index and fecundity data has demonstrated definite spawning periodicity in Agosia chrysogaster. Populations in Aravaipa Creek reached peak reproductive condition biannually, i.e. spring (February through April) and late summer (September) (Table 7, Fig. 5). Although females were gravid with mature (Class II) ova throughout the year, ripe ova (Class I) were only present during February, March, September, and October (Tables 6, 9; Fig. 6). The highest concentration of active nest sites also occurred during those periods. Individual females were capable of spawning at any time during the year, but most reproductive activity by the population was between February and October. Adult males were tuberculate in all sampling periods. The fact that maturity conditions varied widely within each monthly sample indicated that individual spawning activity was asynchronous, and prevented determination of individual spawning duration and time interval between successive spawns.

Photoperiod and water temperature are traditional factors attributed with regulating teleost gonadal cycles in temperate zones (Hoar 1957, Nikolsky 1963). Other factors which may influence reproductive condition and periodicity include food availability (Nikolsky 1963) and stream discharge (John 1963). Suitable external stimuli may act alone or synergistically to induce reproductive readiness. Typically, external conditions act through activation of the endocrine function in the brain. Environmental conditions perceived by sensory receptors stimulate hypothalmic neurosecretory cells to produce gonadotropic hormones, which initiate development of

gonads and reproductive behavior (Pickford and Atz 1957). Thermal regime and food availability act through changes in total metabolic rate.

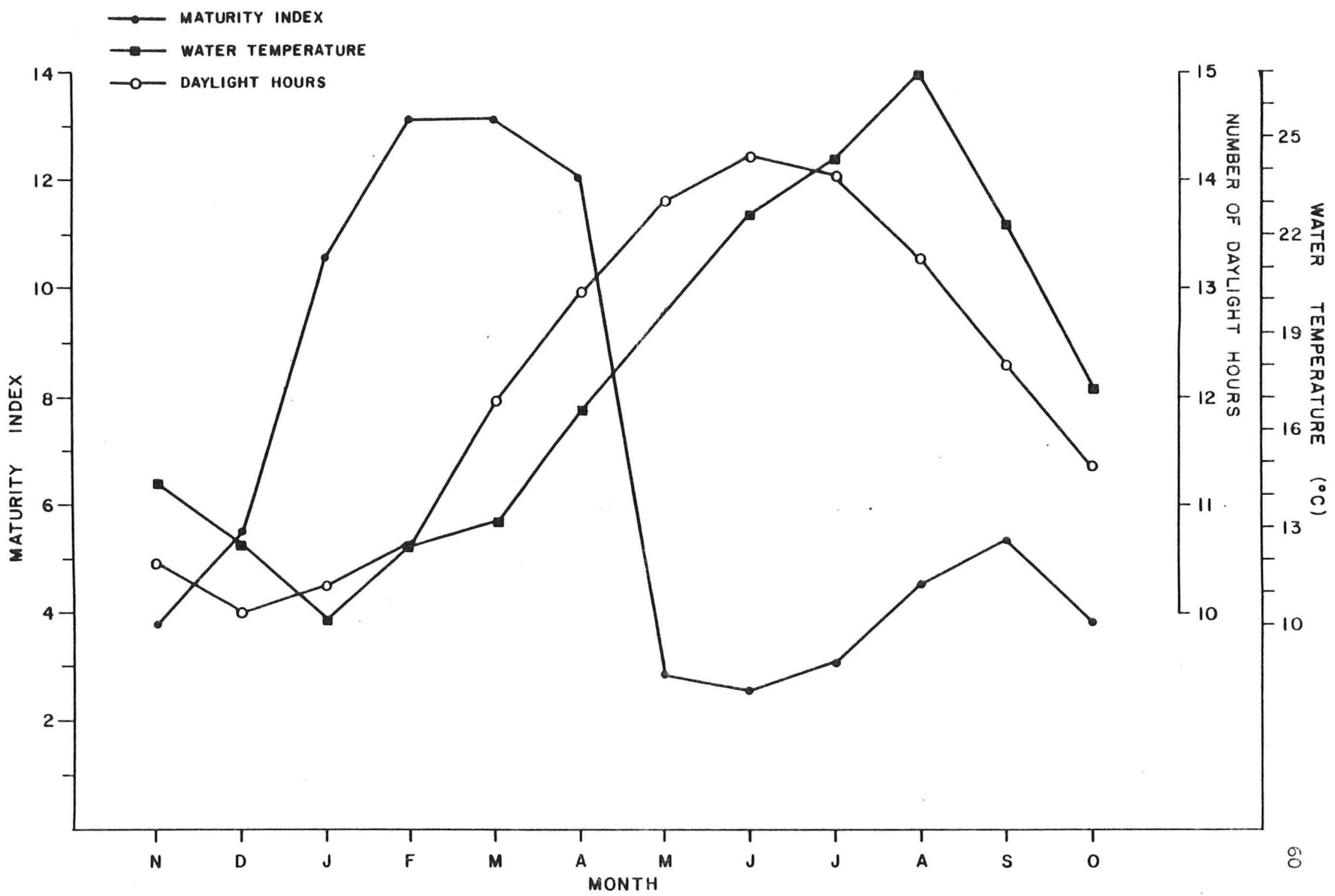
The bimodal spawning habit of A. chrysogaster contrasts markedly with those of temperate-zone fishes, which typically exhibit a single spawning peak in spring or early summer (Nikolsky 1963, Breder and Rosen 1966). Longfin dace spawned on both increasing and decreasing photoperiods (Table 11, Fig. 13), contrary to models developed by Rowan (1938) and Harrington (1957, 1959) for native fishes in the Northern Hemisphere. Maturity indices increased with photoperiod in spring and subsided prior to maximum daylengths in summer. The most active spawning period was when mean daily photoperiods averaged 11.9 hours (February through April). The lowest mean maturity indices were in June when mean daylength was a maximum of 14.2 hours. Indices increased gradually in July and August as a second complement of ova matured toward Classes I and II. The second spawning peak in September was when mean daylength had declined to 12.3 hours.

Mean maturity indices' relationship to water temperatures closely paralleled that for photoperiod (Fig. 13, Table 11). Dace spawned in spring when water temperatures were rising and in late summer when temperatures, like photoperiod, were declining. Most spring spawning was when daily water temperatures averaged 14.2° C. Mean daily maximum and minimum temperatures during that period ranged from 14.4 to 18.6° C and 7.5 to 15.5° C, respectively. Maturity indices were lowest when mean daily water temperatures were above 22.6° C (June through August). Longfin dace spawned in September when water

Table 11. Ambient environmental conditions of Aravaipa Creek, Arizona, 1977-78 (Bulk 1976, USGS 1978, 1979a, Minckley 1981).

Date	Mean Daylight Hours/Day	Mean Water Temperature (^{o}C)	Mean Discharge (m^3/s)
November	10.47	14.33	0.30
December	10.00	12.48	0.30
January	10.26	10.15	1.12
February	10.62	12.68	2.19
March	11.97	13.10	6.43
April	12.97	16.58	0.43
May	13.81	--	0.38
June	14.23	22.63	0.34
July	14.03	24.35	0.48
August	13.29	26.88	1.06
September	12.33	22.38	0.34
October	11.36	17.28	0.24

Figure 13. Comparison of mean monthly maturity indices to mean monthly photoperiod (daylight hours/day) and water temperature (^{o} C), 1977-78, Aravaipa Creek, Arizona. Data on physical features are from Bulk (1976) and Minckley (1981), respectively.


MATURITY INDEX
WATER TEMPERATURE
DAYLIGHT HOURS
MATURITY INDEX
14
12
10
8
6
4
2
NUMBER OF DAYLIGHT HOURS
15
14
13
12
11
10
WATER TEMPERATURE (°C)
25
22
19
16
13
10
N
D
J
F
M
A
M
J
J
A
S
O
MONTH

temperatures first began to decline and mean daily water temperatures fell to 22.4° C. Spawning activity leveled by October and gonads again started to develop in November. The most accelerated gonadal development was in December and January prior to the spring spawn. Water temperatures for that period averaged 11.3° C.

Food availability affects metabolic rate and reproductive condition of females. Calendar periods of spawning also are adapted to insure that larvae will be provided with food during the first stages of external feeding (Nikolsky 1963). Food availability and consumption by adult A. chrysogaster in Aravaipa Creek is greatest in winter and spring, during maximal gonadal development, and least in summer (Schreiber 1978) (Table 12, Fig. 14). Feeding patterns most closely followed patterns in ephermopteran nymph abundance, particularly those of the Baetidae. The dace relied more heavily on a diet on unattached filamentous green algae, e.g. Mougeotia and Spirogyra, in summer following winter and spring mayfly emergence and depletion of invertebrate populations by summer floods. Fry presumably feed in backwater areas on diatoms and detritus, which are abundant in the stream shortly following even severe flooding (Minckley 1981).

Spawning in A. chrysogaster appeared most closely synchronized with flooding events that occurred within the Aravaipa drainage in 1977-78. Most spawning activity was during (or following) elevated flows in spring when stream discharge averaged greater than 3.0 m^3/s (Fig. 15). Maturity indices decreased following declining discharge in early summer and reached their lowest value when mean discharge attained a minimum of 0.34 m^3/s in June (Table 11). The secondary

Table 12. Seasonal differences in total biomass of drift (mg/m^3), benthos (g/m^2), and percentages of total stomach volumes in Agosia chrysogaster for all invertebrate groups from Aravaipa Creek, Arizona, 1975-76 (recalculated from Schreiber 1978, Tables 2, 3, and 5).

Date	Total Drifting (mg/m^3)	Total Benthic (g/m^2)	Total Stomach Volume (%)
April	40.5	3.47	22.8
July	14.8	1.95	4.7
October	28.2	5.59	6.2
January	43.4	16.92	29.5

Figure 14. Comparison of mean monthly maturity indices to seasonal differences in total biomass of drift (mg/m^3), benthos (g/m^2), and percentages of total stomach volumes in Agosia chrysogaster for all invertebrate groups from Aravaipa Creek, Arizona (adapted from Schreiber 1978).

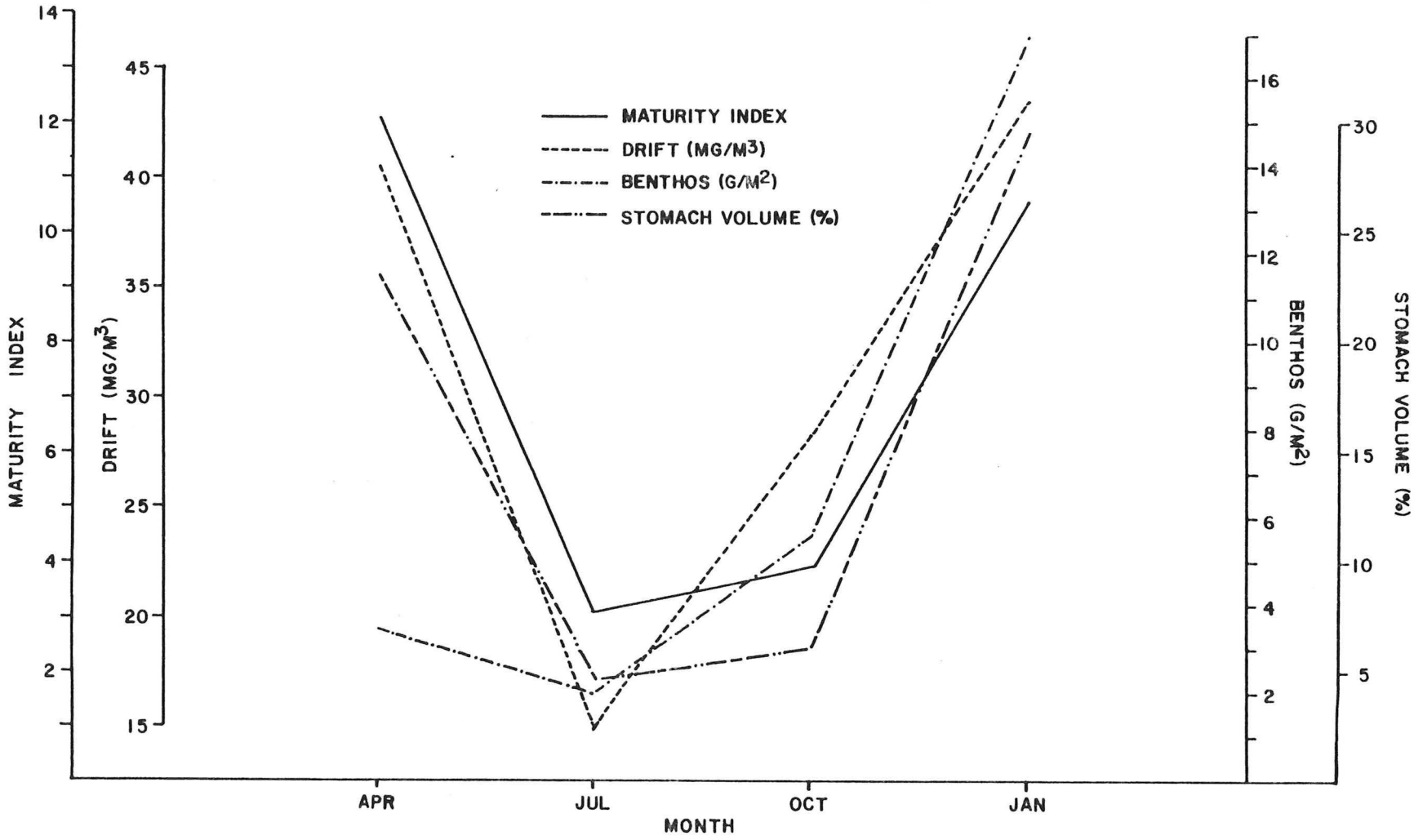
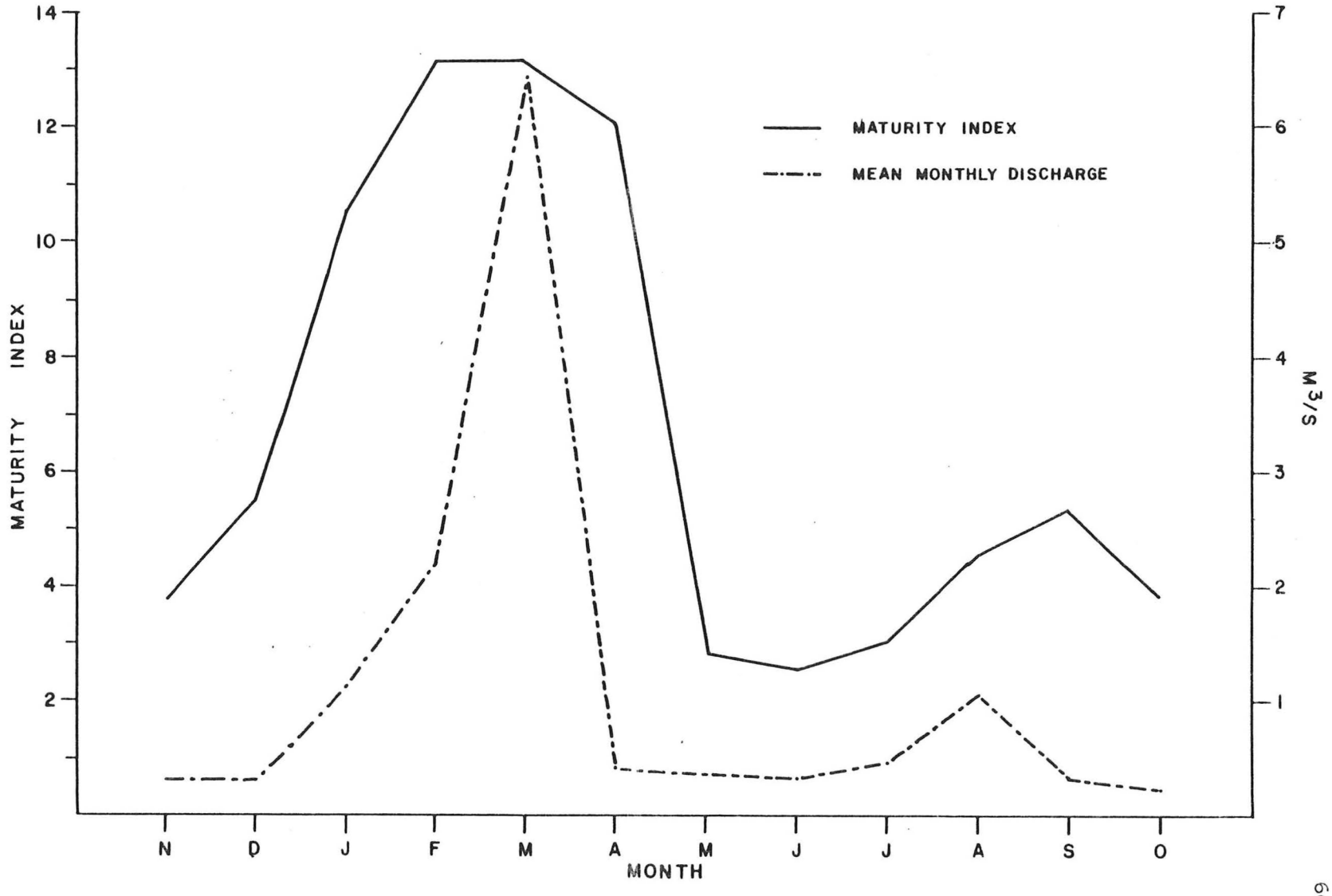

MATURITY INDEX
DRIFT (MG/M3)
BENTHOS (G/M2)
STOMACH VOLUME (%)
MATURITY INDEX
DRIFT (MG/M3)
BENTHOS (G/M2)
STOMACH VOLUME (%)
APR
JUL
OCT
JAN
MONTH

Figure 15. Comparison of mean monthly maturity indices of Agosia chrysogaster to mean monthly discharge (m^3/s), 1977-78, Aravaipa Creek, Arizona.


MATURITY INDEX
MEAN MONTHLY DISCHARGE
MATURITY INDEX
M3/S
MONTH
N
D
J
F
M
A
M
J
J
A
S
O
14
12
10
8
6
4
2
7
6
5
4
3
2
1

spawning peak in Sept mber followed late summer thundershowers and spates that characterize the climatic pattern of the Sonoran Desert. Mean discharge rose to 1.06 m^3/s in August then declined through September and October.

Spawning in response to rainy season floods is characteristic of tropical and subtropical species of fishes (Lowe-McConnell 1975). For example, gonad weights of Ningu (Labeo victorianus) in Lake Victoria reached sexually mature proportions approximately a month prior to the two periods of maximum rainfall, March and September (Cadwalladr 1965). Longfin dace therefore respond like subtropical species in that its bimodal spawning frequency closely parallels the biannual rain pattern.

Few investigators have reported biannual spawning periodicity in desert fishes and others have only alluded to the fact. Koster (1957) first implied spring and autumn spawning for A. chrysogaster and Rio Grande mountain-sucker (Pantosteus plebeius) in New Mexico. John (1963) found that speckled dace (Rhinichthys osculus) in southeast Arizona exhibited a bimodal spawning pattern with discrete spring and late summer peaks following seasonal rains. The dace failed to spawn in summer in the absence of floods. Colorado River spinedace (Lepidomeda vittata) spawn more than once a year beginning in June and ending in October (Minckley and Carufel 1967). Spawning in White River springfish (Crenichthys baileyi) from three thermal springs in Nevada was protracted throughout the year with bimodal peaks occurring in June through August and October through December (Espinosa 1968).

No doubt other southwestern fishes exhibit similar patterns of spawning, but we yet lack confirmation of regional, multiple spawning cycles.

Available evidence further indicates that A. chrysogaster has an individual reproductive strategy unlike most temperate North American fishes, which typically exhibit more clearly defined spawning seasons and produce eggs in a single batch ("total spawning"). Fractional, prolonged spawning in longfin dace is again more characteristic of tropical and subtropical species that reproduce throughout the year. Few species exhibit fractional spawning in temperate latitudes and in the Arctic it is completely absent (Nikolsky 1963). Adaptive advantages of fractional spawning include adjustment to increased food supplies in areas where seasonal changes in day length and water temperature are minimal (subtropic and tropic latitudes). Generally, spawning is more protracted at latitudes where young are suitably provisioned over a considerable part of the year (Nikolsky 1963). Fractional spawning also ensures continuation of a species under unfavorable abiotic conditions that may limit or eliminate results of the spawning adults, e.g. drastic fluctuations in water level. Therefore, longfin dace may take yearlong reproductive advantage of the mild, subtropical climate of the Sonoran Desert and survive reproductive catastrophes otherwise associated with flash flooding in erosional streams.

Factors not investigated include the combined role of inter- and intraspecific competition on spawning periodicity, egg size, and fecundity in longfin dace. Svardson (1949), in his review of natural

selection and egg numbers in fishes, postulated egg numbers are inversely related to competitive intensity, particularly for available food supplies. Density-dependent mechanisms may also regulate spawning periodicity and egg size as well. Hubbs and Johnson (1961) presented evidence that egg number in dusky darter (Percina sciera) increased with reduced intraspecific competition and increased interspecific competition. It is not known what selection pressures are placed on A. chrysogaster reproduction in Aravaipa Creek by the native species that coexist in the system. Individual niches are segregated so that local distribution, behavior, reproduction, and food habits rarely overlap (Deacon and Minckley 1974, Minckley 1981, Schreiber and Minckley 1982). Food resources are also presumably partitioned between adult and young-of-the-year longfin dace and would represent insignificant selective pressures to their reproduction. Aravaipa Creek has continuously yielded high standing crops of longfin dace both in times of drought and flood (Minckley 1981). They have dominated the drainage in numerical abundance and are the first to colonize new stream reaches made available during periods of excessive runoff (Deacon and Minckley 1974). Although competition for availale food supplies does not appear to suppress reproduction in longfin dace, empirical verification of density-dependent factors is lacking and would be difficult to adequately assess (Andrewartha 1961). Additional research is needed to further elucidate the problems of inter- and intraspecific competition and their impact on reproduction.

SUMMARY

1. Adult male and female longfin dace (Agosia chrysogaster) are sexually dimorphic and can be distinguished from each other based on coloration, size and appearance of the urogenital papilla, and morphological differences in dorsal, pelvic, pectoral, and anal fin length. Meristic characters were similar, although nuptial tubercle location and intensity varied between sexes. Females were rarely tuberculate whereas some adult males were in tuberculate condition throughout the entire year.
2. Longfin dace nests are built in open areas cleared of plant debris and located in connected backwaters or over shallow, sand-bottomed runs with laminar flow. Nests take the form of saucer-shaped depressions constructed in fine sand to coarse gravel. No territorial behavior is exhibited by either sex at the nest site.
3. Most longfin dace mature sexually within a year after hatching and reach the size of first maturity at 42.1 mm standard length.
4. Ova are withdrawn for maturation from the general ova stock as distinct batches. Egg classes are generally intermixed throughout the ovary with no visible signs of segregation other than prior to spawning, when Class I ova are concentrated ventroposteriorly near the oviduct.
5. Maturity conditions varied widely within each monthly sample indicating individual spawning to be asynchronous.
6. Individual female longfin dace in Aravaipa Creek are gravid with mature ova throughout the year and therefore capable of spawning

on a yearlong basis. They thus exhibited a protracted reproductive cycle typical of tropical and subtropical fish species.

7. Although individual spawning activity is asynchronous, mean maturity index and fecundity data indicate that longfin dace populations in Aravaipa Creek reach peak spawning condition semiannually, i.e. spring (February through April) and late summer (September).

8. Fecundity is positively correlated with fish length, weight, ovary weight, and maturity index and therefore is a function of size.

9. Ovary weight is the most highly correlated variable to egg number and therefore the best indicator relative to total fecundity. Fish length was the least reliable index to fecundity.

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BIOGRAPHICAL SKETCH

William George Kepner was born in Ravenna, Ohio, on 29 March 1952. In 1956, he moved with his family to Phoenix, Arizona, where he received his elementary and secondary educations at the Osborn School District and West Phoenix High School. In 1970, he entered Phoenix Community College and was awarded an Associate of Arts degree with honors in 1972. In January 1973 he entered the University of Arizona in Tucson. He graduated in 1975 with a Bachelor of Science degree with honors in Biology. From 1975 to 1976 he worked for the Lower Colorado River Basin Research Laboratory, Arizona State University, and in 1977 was employed by the U.S.D.A. Forest Service. In 1976, he entered the Graduate College at Arizona State University. While studying for a Master of Science degree in Zoology, he conducted wildlife/fisheries inventories in western Arizona for the U.S.D.I. Bureau of Land Management, Phoenix District Office. In 1980, he received a Unit Citation Award for Excellence of Service from the Secretary of the Interior for his performance in conducting vertebrate inventories on public lands. He received the Doug Morrison Memorial Award from the Arizona Chapter of the Wildlife Society and was acknowledged as the Outstanding Wildlife Biologist in Arizona for 1981. He is currently a Wildlife Biologist for the U.S. Bureau of Land Management and is married to Lauren Porzer Kepner, a wildlife biologist for the Arizona Game and Fish Department and Master of Science graduate from the Department of Zoology at Arizona State University.